
MODELLING THE INFLUENCE OF WEED COMPETITION ON
GROWTH OF JUVENILE *PINUS RADIATA* AT A DRYLAND SITE

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submitted in partial fulfilment
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By

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Pinus radiata D.Don trees growing in plots with (arrowed left) and without broom (right) at the experimental site, two years after planting. The ruler on the left side is 1m.

ABSTRACT

The reduction in growth of commercially grown conifers by weeds over the juvenile phase is an important management issue. This thesis investigates the mechanisms of interaction between juvenile *Pinus radiata* and the woody weed broom (*Cytisus scoparius* L.) at a dryland site, and uses this information to develop process-based models of tree growth, sensitive to competition from weeds. All the results presented in this thesis were taken from an experiment established on a drought prone site, located on the Canterbury Plains, New Zealand. Within the experiment a comprehensive and detailed set of measurements were taken from trees growing weed-free and with broom competition, from the beginning of the second year to the end of the third year after planting.

The presence of broom severely retarded the growth of trees over the two year measurement period. Treatment differences in basal area, which became significant one month after measurements started, increased from six-fold at the end of the first year to 12-fold after two years. At the end of the second year, trees growing without broom were two-fold taller, and had a crown diameter four-fold greater than trees in plots with broom. Above-ground biomass was the most sensitive indicator of competition. Compared to trees in weed-free plots, above-ground biomass of trees in plots with broom was reduced by 25-fold after two years.

During the first year, the strong link between predawn needle water potential, ψ_e , and fractional biomass growth for trees in plots with broom ($r^2=0.91$) suggests growth losses in this treatment were almost entirely attributable to seasonal water deficit. Although ψ_e was also strongly related to fractional biomass growth, f_b , over the second year ($r^2=0.71$), values of f_b across a comparable range of ψ_e , were on average 15% lower than during the first year. Inclusion of a simple shading index explained this difference, suggesting broom restricted tree growth during the second year through competition for both light and water.

Nitrogen fixation by broom, and the extent of fixed nitrogen transfer to *Pinus radiata* was assessed from measurements of the natural abundance of the ^{15}N isotope, $\delta^{15}\text{N}$. Values of $\delta^{15}\text{N}$ were highest in *Pinus radiata* growing without broom, intermediate

in *Pinus radiata* growing with broom, and lowest in field grown broom. Broom was an effective fixer, deriving 81% of nitrogen in above-ground tissues from the atmosphere, which was equivalent to $111 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The intermediate values of $\delta^{15}\text{N}$ found for trees growing with broom suggest that there was some transfer of fixed nitrogen from the broom to the *Pinus radiata*. However as soil uptake by the broom ($29 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) considerably exceeded estimated rates of nitrogen transfer ($2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) growth of trees was not enhanced by this recycling of fixed nitrogen.

Compared with *Pinus radiata* in weed-free plots, trees growing with broom allocated dry matter preferentially to stems (+8%) at the expense of foliage (-4%), roots (-2%) and branches (-2%). These findings on allocation confirm derivations based on pipe model theory and indicate that the root to shoot ratio in juvenile *Pinus radiata* remains relatively stable even under severe water deficit.

A water balance model was developed to partition water loss and explain treatment differences in tree basal area growth, over the first year. In both treatments, modelled root-zone water storage (W) corresponded closely to measured values over the course of the year. Total annual evaporation in the treatment with broom was 25% higher than that for the treatment without broom. This higher rate was primarily due to wet canopy evaporation from the broom and, to a lesser extent, from increased rates of total transpiration within this treatment. The integral of root-zone water deficit was strongly related to fractional basal area growth of trees in plots with broom. These findings highlight the importance of root-zone water storage in regulating productivity on dryland sites and indicate that water balance modelling provides a useful approach for predicting the influence of weed competition on tree growth.

A generally applicable model of juvenile tree growth was developed and tested at this dryland site. This model predicts tree growth by reducing growth from an empirically determined optimum rate (weed-free) using a seasonally estimated competition modifier, which accounts for the degree of weed competition for both water and light. Test results showed good correspondence between measured and predicted tree diameter growth in treatments with and without broom, over the two year period. As this model was developed using process-based modifiers for water and light it is applicable to sites covering a wide range of climatic and edaphic conditions.

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LIST OF SYMBOLS

Symbol	Description	Units
A_b	<i>Pinus radiata</i> groundline basal area	$\text{m}^2 \text{ tree}^{-1}$
A_d	<i>Pinus radiata</i> groundline diameter	mm
A_f	<i>Pinus radiata</i> foliage area	$\text{m}^2 \text{ tree}^{-1}$
B	$\delta^{15}\text{N}$ of broom growing under fully symbiotic conditions	‰
c	Fractional stone content of the soil	$\text{m}^3 \text{ m}^{-3}$
c_l	Competition index for light	-
c_w	Proportion of non-crop cover within 1 m radius of tree	-
D	Air saturation deficit	kPa
D_{0b}	Sensitivity of broom g_{sb} to D	kPa
D_{0t}	Sensitivity of <i>Pinus radiata</i> g_{st} to D	kPa
D_{smin}	Value of D below which g_s is constant	kPa
E_b	Transpiration from the broom canopy	mm
E_{bw}	Evaporation from the wet broom canopy	mm
E_g	Evaporation from the soil surface	mm
E_t	Transpiration from the <i>Pinus radiata</i> canopy	mm
E_{tw}	Evaporation from the wet <i>Pinus radiata</i> canopy	mm
F	Drainage from the root zone	mm
f_b	Fractional biomass growth	-
G	<i>Pinus radiata</i> biomass growth	g
G_a	Available energy above the canopy	$\text{MJ m}^2 \text{ day}^{-1}$
G_g	Available energy beneath the tree and broom canopies	$\text{MJ m}^2 \text{ day}^{-1}$
G_i	Initial biomass of <i>Pinus radiata</i>	g
g_{sb}	Broom stomatal conductance	$\text{mmol m}^{-2} \text{ s}^{-1}$
g_{st}	<i>Pinus radiata</i> stomatal conductance	$\text{mmol m}^{-2} \text{ s}^{-1}$
g_{sbmax}	Broom maximum stomatal conductance	$\text{mmol m}^{-2} \text{ s}^{-1}$
g_{stmax}	<i>Pinus radiata</i> maximum stomatal conductance	$\text{mmol m}^{-2} \text{ s}^{-1}$
h_b	Average broom height within 1m radius of tree	mm
h_t	<i>Pinus radiata</i> height	mm
h_r	h_b/h_t	-
k	Light extinction coefficient	-
l	Mean needle length	mm
l_i	Maximum rate of needle growth	mm day^{-1}
l_m	Maximum needle length	mm
L_b	Broom leaf area index	$\text{m}^2 \text{ m}^{-2}$
L_t	<i>Pinus radiata</i> leaf area index	$\text{m}^2 \text{ m}^{-2}$
m_c	Combined competition modifier	-
m_l	Competition modifier for light	-
m_w	Competition modifier for water	-
[N]	Nitrogen concentration	mg g^{-1}
P	Precipitation	mm
r	Root zone depth	mm

Symbol	Description	Units
s	Slope of the relationship between saturated vapour pressure and temperature at a given air temperature	kPa °C ⁻¹
$s(t)$	Seasonally adjusted time	years
S_{ψ}	Water stress integral	MPa day
S_w	Integrated root-zone water deficit	mm
t	Time after reference date	days
t_{95}	Time taken for needles to reach 95% of maximum length	day
t_i	Time at which maximum rate of needle growth occurs	day
t_m	Time when growth reaches a maximum	years
t_0	Reference starting point	day
W	Root-zone water storage	mm
%Ndfa	Percentage of nitrogen derived from the atmosphere	-
$\delta^{15}\text{N}$	Nitrogen isotope composition	‰
$\delta^{15}\text{N}_{\text{ag}}$	Isotopic mass balance of aboveground tissues	‰
$\delta^{15}\text{N}_{\text{ref}}$	$\delta^{15}\text{N}$ of reference plant (<i>Pinus radiata</i> in weed-free plots)	‰
$\delta^{15}\text{N}_{\text{fix}}$	$\delta^{15}\text{N}$ of fixer (broom)	‰
γ	Psychrometric constant	kPa °C ⁻¹
λ	Latent heat of vaporisation	J kg ⁻¹
θ	Root-zone volumetric water content	m ³ m ⁻³
θ_a	Fractional available root-zone volumetric water content	-
θ_{max}	Maximum root-zone volumetric water content	m ³ m ⁻³
θ_{min}	Minimum root-zone volumetric water content	m ³ m ⁻³
θ_t	Value of θ when E_t , E_b , E_g decline	m ³ m ⁻³
τ	Degree of coupling of soil surface to air above canopy	-
ω	Amplitude of the seasonal growth	-
ψ	Needle water potential	MPa
ψ_e	Predawn needle water potential	MPa

CHAPTER ONE

GENERAL INTRODUCTION

INTRODUCTION

Background

In plantation forestry, the period of establishment is a time of opportunity for forest managers to influence the long term productivity of the crop. Correct decisions made at this stage regarding selection of species (Evans, 1992), genotype (Shelbourne, 1986), handling and planting practice (Mason, 1985), land preparation (Mason and Cullen, 1986) and vegetation management (Richardson, 1993) can have profound effects on future survival, harvest volumes and profit margins (Richardson, 1993; Mason, 1996). Vegetation management plays a critical role in stand establishment and, as a management practice, is often the most influential on the rate of early crop growth (Mason and Whyte, 1997; Zhao, 1999).

Vegetation management has been defined as the practice of efficiently channelling limited site resources into the crop rather than co-occurring non-commercial species (Walstad and Gjerstad, 1984). Although this is unquestionably the main purpose of this practice, there are several secondary considerations this definition does not include. Competing vegetation may also adversely influence crop growth through parasitism (Minko and Fagg, 1989), alleopathy (Maclaren, 1983), and physical damage. In addition, vegetation management is frequently undertaken to reduce the risk of frost damage (Menzies and Chavasse, 1982) and fire hazard (Burrows *et al.*, 1989). Although these secondary factors may be important in certain situations, reported reductions in tree growth have been primarily attributed to competition by weeds for light, water and nutrients (Richardson, 1993). A reduction in the availability of these site resources restricts physiological processes such as leaf area development, carbon assimilation, stomatal conductance and water use efficiency (Boomsma and Hunter, 1990).

The beneficial influence of vegetation management has been widely documented for a range of commercially grown tree species. Almost all studies report large volume

gains, ranging from 25-fold one year after planting to 80% after 10 years. The influence of weed competition declines with increasing crop age as closure of the tree canopy usually retards growth of the often shade intolerant competition. Inducement of water stress by weeds may also be reduced with age as trees access sources of water deeper in the profile (Sands and Nambiar, 1984). Although long-term weed control studies are relatively rare, there is some evidence to suggest growth gains obtained during the juvenile phase are maintained throughout the rotation (Snowdon and Khanna, 1989; Balneaves and McCord, 1990; Mason and Milne, 1999).

Given the large influence of weeds on initial tree growth, it is important that managers have access to the right information in order to make informed decisions regarding vegetation management. The cost-benefit ratio of any treatment applied to reduce competition depends on (1) treatment efficacy (2) treatment costs (3) the influence of the treatment on final crop volume and (4) final crop value. Of these factors, the effect of treatment on long term growth is most difficult to define (Walstad and Kuch, 1987), as it depends on a range of influences including weed species, weed density, tree age, and site conditions.

Given the complexities involved in estimating the effects of competition on long term growth, development of a generally applicable juvenile growth model, sensitive to weed competition would provide a useful decision tool for managers. A model of this type, which can be linked into growth models for older trees, would allow the cost-effectiveness of alternative vegetation management regimes to be quantified. Prior to discussing the most appropriate form of these juvenile growth models, the main types of growth models used in forestry are first outlined.

Approaches to modelling tree growth

Forestry growth models can be categorised according to their level of mechanistic detail, complexity, and generality (Battaglia and Sands, 1998). At one end of the scale are the conventional empirical forestry models, which use regression techniques to derive growth equations which best fit the observed data. These data commonly include measurements of tree number, stem diameter, and height. While these models contain no explicit representations of the interception of solar radiation, water use or carbon

allocation, they are widely used by managers as they are simple to parameterise and provide reasonably accurate predictions of tree growth. However, such models are often limited in their general applicability and do little to elucidate the mechanisms of tree growth.

In contrast, process-based models are more soundly based on the mechanisms which underlie tree growth. As these models are responsive to changes in environmental and site conditions they are more generally applicable than empirical models. However, these models are seldom used as practical tools in forest management as they include too many uncertainties and often require values for a large number of parameters which are difficult to obtain (Mäkelä *et al.*, 2000). Despite this, there has recently been much interest in applying process-based models to management applications, using simplified relationships developed from more detailed models (Landsberg and Waring, 1997). In the future, it is likely that management based models will include more process-based components, to improve the general applicability of predictions (Mäkelä *et al.*, 2000).

Hybrid models contain elements of process-based and empirical models. These models incorporate a mechanistic description of environmental influences into an empirical growth and yield model. Hybrid models provide an increase in biological realism over traditional empirical growth models, yet do not require the level of parameterisation of process-based models (Mäkelä *et al.*, 2000).

Growth modelling during the juvenile phase

Despite their potential utility as a management tool, there have been very few juvenile growth models developed to date. Early crop growth of a range of conifers in the western USA has been modelled empirically (Payendeh, 1987; Belli and Ek, 1988). More recently, empirical models of juvenile *Pinus radiata* growth have also been constructed for both wet (Mason and Whyte, 1997; Mason, 2001) and dryland sites (Zhao, 1999) within New Zealand. Although these models showed weed control to be the single most important management treatment for improving tree growth and survival, their insensitivity to weed species and level of weed cover was recognised (Mason and Whyte, 1997).

Development of more biologically realistic growth models requires specific knowledge of the mechanisms of interaction between trees and competitors. Although the general principles by which weeds retard tree growth are known, the interactions between trees and weeds for specific sites are poorly documented (Richardson *et al.*, 1996). One approach to understanding these interactions is to investigate how weeds alter resource availability and how the trees respond to this change in resource availability (Goldberg, 1996).

Using this approach, mechanisms of juvenile tree suppression by a range of common weed species were investigated on a wet, fertile site in the Central North Island (Richardson *et al.*, 1996). It was found that tall, fast growing weed species on this site reduced *Pinus radiata* growth through restriction of solar radiation reaching the tree crowns. No convincing evidence was found to link the observed growth losses with competition by weeds for water or nutrients (Richardson *et al.*, 1996).

Data from this trial were used to develop a hybrid juvenile growth model sensitive to weed competition. Tree growth was successfully modelled from planting to age three, by reducing growth from an empirically determined optimum rate (weed-free) using a competition modifier which essentially described the degree of weed competition for light (Kimberley and Richardson, 2001). Although this model is suitable for wet sites, where weeds restrict growth primarily through light attenuation, it is not applicable to areas which experience seasonal water deficit.

Previous research indicates that competition by weeds at dryland sites is primarily for water (Nambiar and Zed, 1980; Sands and Nambiar, 1984; Richardson *et al.*, 1997; Bandara, *et al.*, 1999). Water moves from the soil through roots, xylem and leaves along a gradient of decreasing water potential, driven by transpiration. When water supply is not sufficient to meet the atmospheric demand, closure of the stomata will occur, to avoid the development of damaging leaf water potential. Closure of the stomata reduces growth, through limiting rates of carbon assimilation (Whitehead, 1998). Over the longer term, water deficits cause reductions in leaf production and rates of expansion and may induce early leaf loss (Pereira and Chaves, 1993). These effects reduce leaf area, which in turn results in lower growth rates as less light is intercepted by the tree. While it is possible that water deficits may also reduce long-term growth through inducing greater

allocation to non-photosynthetic tissues (roots, stem, branches), the mechanisms for this are uncertain (Landsberg and Gower, 1997), and this topic requires further investigation.

Given the importance of water availability in regulating tree productivity on dryland sites, a water balance approach may be useful for estimation of a modifier for inclusion in the Central North Island hybrid model. The water balance approach calculates water storage in the root-zone from the difference between incoming rainfall and losses due to transpiration, wet canopy evaporation, soil surface evaporation and drainage (Figure 1.1).

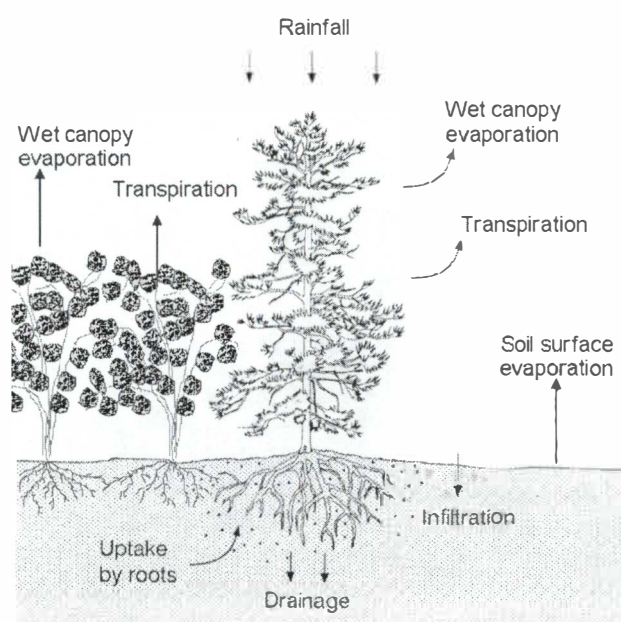


Figure 1.1. Diagrammatic representation of the components of water balance for trees growing with a weed understory. Adapted from Landsberg and Gower, 1997, p. 90.

Water balance models have been used both separately (Richardson *et al.*, 2003) and as components of highly parameterised process-based models (Walcroft *et al.*, 1997; Arneth *et al.*, 1999) to predict growth of mature *Pinus radiata* on dryland sites. However, there have been few attempts to use a water balance modelling approach to predict growth of *Pinus radiata* during the juvenile phase, at which time trees are most sensitive to water stress (Sands and Nambiar, 1984).

AIMS AND SCOPE OF THIS THESIS

Thesis objectives

The objectives of this thesis are to:

- (i) quantify differences in growth and allocation of *Pinus radiata* growing in plots with and without the woody weed broom (*Cytisus scoparius* L.),
- (ii) determine the mechanisms of interaction between *Pinus radiata* and broom,
- (iii) use a water balance modelling approach to (1) investigate which components of water balance are most influenced by presence of the broom and (2) determine if root-zone water storage can explain growth differences of trees in plots with and without broom,
- (iv) develop a generally applicable juvenile growth model, sensitive to weed competition.

Description of selected tree and weed species

Pinus radiata is the most commonly planted tree species in New Zealand occupying 90% of the 1.8 million hectare plantation estate (N.Z.F.O.A., 2002). This conifer is able to flourish on a wide variety of sites as it is frost resistant and drought tolerant. Typically, wood production levels are high, particularly in wet fertile areas, where growth rates of up to $52 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ are reached (Shula, 1989). As this species responds well to silvicultural and environmental manipulation, high rates of productivity are often achieved and maintained through intensive management practices.

Broom is a common introduced shrub widely distributed throughout New Zealand, which has colonised an extensive range of habitats, including large tracts of plantation forest estate. As broom originates from the Mediterranean (Hegi, 1926), it has a number of dry climate adaptations, which include small drought-deciduous leaves, specialised stem photosynthesis and prolific production of long-lived seeds. In addition to these attributes, the ability of broom to grow rapidly and fix nitrogen make it a successful pioneer of open and disturbed habitats, where it commonly forms dense thickets, which can suppress and inhibit growth of newly planted conifer seedlings (Peterson and Prasad, 1998).

Synopsis of experiment

The experiment was located in an existing 1 year old *Pinus radiata* plantation, established near Hororata on the Canterbury plains, New Zealand (Fig. 1.2).

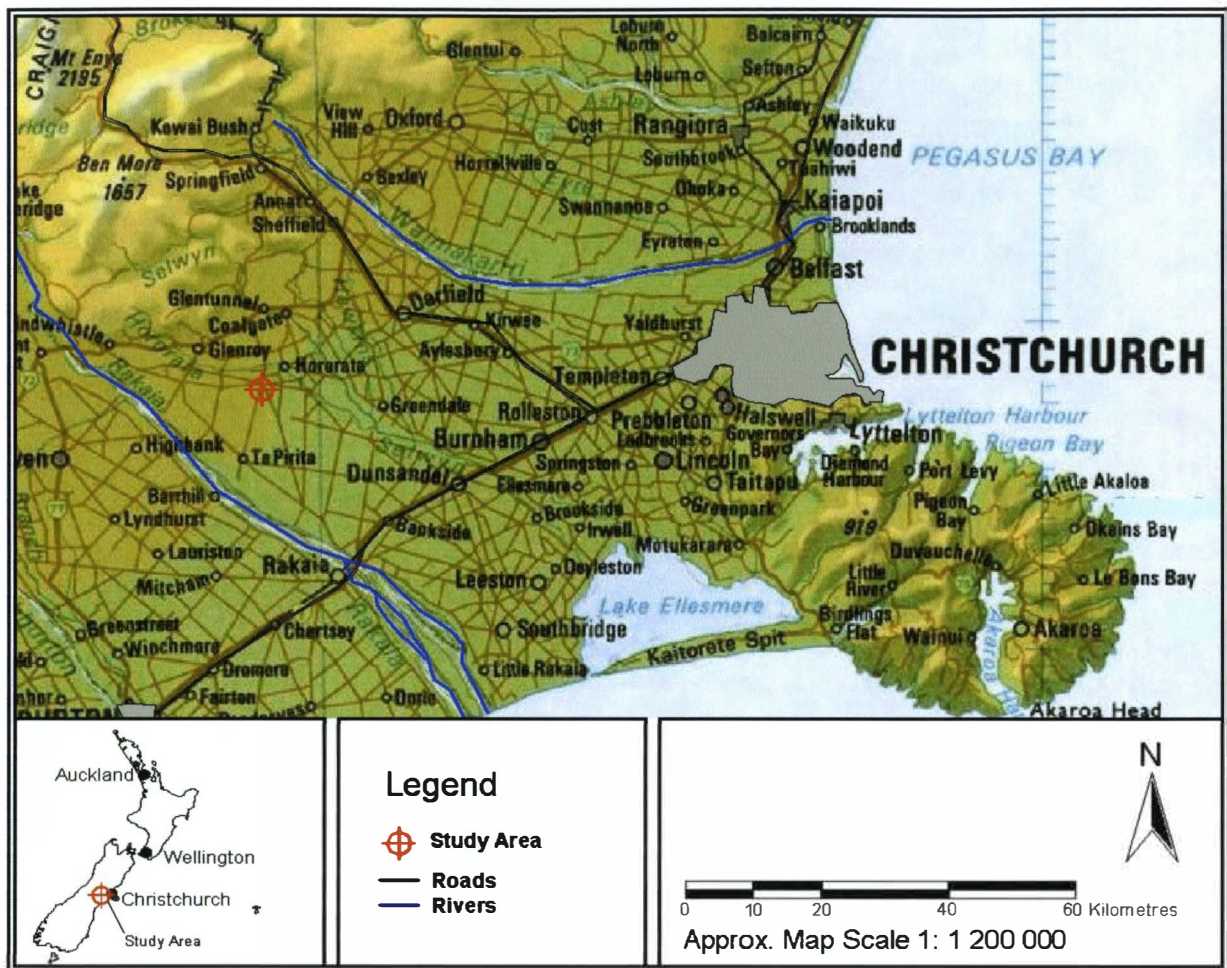


Figure 1.2. Location of experimental site.

This site is representative of a large area of dryland forest with New Zealand, where weeds compete strongly with juvenile trees. Growth rates of *Pinus radiata* on the Canterbury plains are relatively low as this dryland area is prone to severe seasonal water deficits. As is typical management practice for this region, the experimental site had been windrowed before being machine planted with genetically improved (GF 17) seedlings at 1 250 stems per hectare.

During the summer of 1999 twelve plots were established in this plantation in areas where natural broom regeneration was high. These twelve plots were divided into six blocks. Plots within each block were randomly assigned to two treatments, which included no control of weeds and complete removal of weeds. All measurements included in this thesis were taken over the juvenile growth period, from the beginning of the second year to the end of the third year after planting.

Thesis structure

The aim of this thesis is to identify the mechanisms of competition between broom and *Pinus radiata* growing at a dryland site, and use this information to develop process-based models of tree growth. Rather than investigate the influence of a range of weed species under a variety of site conditions, a mechanistic approach has been adopted, using a commonly occurring weed in a representative dryland environment. The advantage of this approach is that once the underlying processes have been defined and modelled they can be readily applied to other sites and weed species.

Although weed induced losses in conifer growth have been attributed primarily to competition for water at dryland sites, very few studies have accurately partitioned the mechanisms of interaction. Chapter Two determines the relative importance of broom competition for water and light using a technique which removes the confounding influences of season and tree size from analyses. These results form the basis of further modelling work.

The second aim of Chapter Two is to investigate how competition from broom influences dry matter partitioning within *Pinus radiata*. Although it is generally assumed that competition for water induces greater biomass allocation to roots, there is very little empirical evidence to support this common perception. The influence of competition for light is also the subject of some controversy. While the pipe model theory (Shinozaki *et al.*, 1964a, 1964b) predicts that high levels of competition for light will induce greater allocation to stemwood, this view is opposed by the priority theory of allocation (Waring and Schlesinger, 1985; Oliver and Larson, 1996) which suggests greater competition for light will increase allocation to foliage, at the expense of stemwood (Waring *et al.*, 1980). Chapter Two addresses how competition for light and water influences allocation using

an analytical technique which separates size dependent changes in allocation from functional adjustments made in response to treatment.

Chapter Three quantifies nitrogen fixation by broom over the first year and investigates if fixed nitrogen transfer occurs between broom and *Pinus radiata* during this period. As broom is an nitrogen fixing weed species, transfer of fixed nitrogen to *Pinus radiata* may partially offset growth losses incurred by broom competition for site resources. Very little research has assessed nitrogen fixation rates by broom and there is no published literature describing recycling of fixed nitrogen between this species and non-fixing conifers.

The water balance approach has been widely used to model root-zone water storage and predict growth in mature conifer stands. However very little research has investigated the utility of this approach in juvenile stands, when water stress is often most limiting to tree growth. Chapter Four investigates the robustness and accuracy of the water balance approach in predicting root-zone water storage for juvenile trees growing with and without competition from broom. Predicted root-zone water storage is related to growth losses for trees growing with broom, to assess the utility of the water balance approach as a process-based model for water competition.

Using insights and results gained from Chapters Two to Four a generally applicable model of juvenile tree growth sensitive to weed competition is developed and tested at this dryland site. Chapter Five presents these results and then uses this model to quantitatively partition the influence of broom competition for water and light on tree diameter growth.

As well as highlighting the key findings of this thesis, Chapter Six also places the results in a wider context, and discusses possible future directions of the modelling work.

Chapters Two to Five have been formatted for publication as individual papers. Chapters Two and Three and Four has been accepted for publication in *Forest Ecology and Management*. Although each chapter stands alone, there is a common thread of investigation evident throughout the thesis. The overarching theme is to determine interactions between *Pinus radiata* and broom, and use this information to develop predictive models of tree growth, sensitive to competition from weeds.

CHAPTER TWO

THE INFLUENCE OF WEED COMPETITION FOR LIGHT AND WATER ON GROWTH AND DRY MATTER PARTITIONING OF YOUNG *PINUS* *RADIATA*, AT A DRYLAND SITE¹

INTRODUCTION

The presence of weeds has been found to reduce growth of a wide range of commercially grown conifers including *Pinus taeda* L., (Knowe *et al.*, 1985), *Pinus palustris* Mill. (Nelson *et al.*, 1985), *Pinus elliottii* var. *elliottii* (Baker, 1973) and *Pinus radiata* D.Don (Richardson *et al.*, 1996). Growth reductions in conifers have been primarily attributed to competition by weeds for water, light and nutrients (Nambiar and Sands, 1993; Richardson, 1993). A reduction in the availability of these site resources restricts physiological processes such as leaf area development, photosynthesis, stomatal conductance and water use efficiency (Boomsma and Hunter, 1990).

At dryland sites, competition by weeds is primarily for water. The presence of weeds has been shown to reduce soil water availability in juvenile stands of *Pinus elliottii* (Baker, 1973) and *Pinus radiata* (Sands and Nambiar, 1984), through increasing rates of total transpiration and wet canopy evaporation (Watt *et al.*, 2003). Needle water potential (ψ) of juvenile conifers has been found to decrease when weeds are present (Sands and Nambiar, 1984), and several studies have demonstrated a linear relationship between percentage cover of weeds and ψ (Nambiar and Zed, 1980; Peterson and Maxwell, 1987).

Measurements of water stress induced by competing vegetation have been related to losses in conifer growth. Most of this research quantifies the intensity and duration of tissue dehydration using the water stress integral, S_{ψ} , which is the cumulative sum over time of predawn needle water potential below a datum. This index, first developed by Myers (1988), explained differences in annual needle elongation and seasonal branch

¹ This chapter is in press with *Forest Ecology and Management* as Watt, M., Whitehead, D., Mason, E.G., Richardson, B. and Kimberley, M.O.

extension of *Pinus radiata* growing with and without lucerne (Bandara *et al.*, 1999). More recently, a variation of the water stress integral using integrated root-zone water deficit was found to be highly correlated with reductions in basal area increment of juvenile *Pinus radiata* growing with broom (Watt *et al.*, 2003).

Although water stress has been implicated as the primary regulator of juvenile conifer growth on dry sites, it is likely that competition for light will also occur when woody weeds are present. Competition for light is likely to increase over the first few years after planting if these woody weeds are tall, fast growing species which can rapidly overtop and shade the conifer. Despite the potential importance of this effect, very few studies have quantified the relative significance of weed competition for light and water when both simultaneously limit tree growth.

Competition by weeds may also influence juvenile conifer productivity through altering patterns of allocation. Relatively little is known about carbon partitioning in juvenile conifer stands, and the influence of competition on tree allometry is the subject of some controversy. The pipe model theory (Shinozaki *et al.*, 1964a, 1964b) predicts that high levels of competition for light will induce greater biomass allocation to stemwood, to maintain a stable ratio between leaf area and stem cross-sectional area. In contrast the priority theory of allocation (Waring and Schlesinger, 1985; Oliver and Larson, 1996) suggests greater competition for light will increase allocation to foliage, at the expense of stemwood (Waring *et al.*, 1980). Although it is generally thought that increased competition for water reduces biomass allocation to shoots (Ryan *et al.*, 1996), a number of studies have demonstrated that the root to shoot ratio remains relatively constant in juvenile trees even under severe water stress (Newton and Cole, 1991; Osório *et al.*, 1998).

Competition studies frequently misinterpret treatment influences on growth and allocation as results are confounded by treatment induced differences in tree size. It has been widely documented that as juvenile conifers develop there is an increase in partitioning to woody tissues, which is accompanied by a parallel decline in allocation to foliage (Cannell, 1985). As trees in weed free plots almost invariably exhibit higher growth rates than trees growing with weed competition, comparisons of allometry made at the same age may reflect size dependent rather than treatment differences.

Confounding also commonly occurs when quantitative relationships between resource availability (e.g., water) and tree growth rate are developed. Although these relationships often use time series data, the influence of initial tree size is not generally removed, despite the large effect of this variable on annual tree growth (Mason, 2001; Watt *et al.*, 2003).

In this study, functional growth analysis is combined with allometric regression and growth modelling techniques to remove the confounding influence of tree size from the analyses. This study aims to quantify the effect of broom (*Cytisus scoparius* L.) competition for light and water on the growth and biomass allocation of young *Pinus radiata* growing at a dryland site.

METHODS

Site description and treatments

Measurements were made over a two year period beginning June 2000 in a 1 year old *Pinus radiata* plantation located near Hororata (latitude 43° 34' S, longitude 171° 55' E, elevation 210 m asl) 60 km west of Christchurch, New Zealand. The soil at this site, which is classified as a Lismore stony silt loam, is shallow, free draining and of low fertility (Kear *et al.*, 1967). Seasonal water deficits are characteristic of this soil and very common near Hororata as long term average rainfall is low (797 mm yr⁻¹) and evaporative demand over spring and summer high (New Zealand Met. Service, 1983).

Plots were located within a 20 ha *Pinus radiata* plantation established during winter 1999, at a spacing of 4 x 2 m (1 250 stems ha⁻¹). During the summer of 1999 twelve plots were established in areas where natural broom regeneration was high. The twelve plots were divided into six blocks. Plots within each block were randomly assigned to two treatments, which included no control of weeds and complete removal of all weeds. Each plot was approximately 12 x 24 m and included an interior 24 measurement trees, completely surrounded by buffer rows of seedlings.

Weed control was achieved by applying 6.25 kg of terbuthylazine mixed with 900 g of clopyralid and 300 g of haloxyfop in 250 l ha⁻¹ of water. This herbicide was applied annually to designated plots to eliminate existing vegetation, which consisted

mainly of broom, interspersed with some herbaceous broadleaved weeds. Weed re-growth during intervening periods was removed by a combination of hand weeding and spot herbicide application.

A tipping bucket raingauge on a 1.5 m stand recorded precipitation above the broom and *Pinus radiata* canopy.

Tree and broom growth

Tree groundline diameter, height and crown width were measured at monthly intervals. At the same time, height of the tallest eight broom plants surrounding the tree was measured and averaged. Mean relative height (h_r) was calculated as the ratio of average broom height to tree height.

Leaf area index of the broom, L_b , was estimated using a canopy analyser (LAI-2000, Li-Cor Inc., Lincoln, NE, USA) at intervals of approximately one month. Plots were stratified into between and within row components as the influence of a strip herbicide applied after planting was still apparent. L_b was measured at 24 locations randomly selected within each component, and these plot level estimates were modelled against time using a segmented regression procedure (Hunt, 1982). Seasonal estimates of L_b for the entire plot were obtained by averaging modelled values for both components.

Predawn needle water potential

Measurements of predawn needle water potential (ψ_e) were made every two weeks using a pressure chamber. In each of the six replicate plots, the youngest well-developed foliage was sampled from a minimum of three trees. The fascicles were harvested before dawn, stored in test tubes on ice and ψ_e was measured three to four hours later.

Needle growth

Non-destructive measurements of needle expansion were made on ten trees within each treatment. A branch was randomly chosen within each tree, and a datum point signifying the start of the current shoot was marked at the base of the leading bud. Starting in spring the length of randomly selected fascicles was measured over the current

shoot every two weeks until the following winter. Data obtained from individual trees was modelled as a function of the number of days, t , after a reference date immediately prior to elongation by the von Bertalanffy equation (Richards, 1959), as,

$$l = l_m (1 - e^{-a_1 t})^{a_2} \quad (2.1)$$

where l is mean needle length, l_m is the maximum needle length, and a_1 and a_2 are parameters. Differentiation of the von Bertalanffy equation allows the calculation of maximum rate of needle growth at the point of inflexion in the relationship, l_i , and the value of t when this occurs, t_i .

Destructive harvests of *Pinus radiata* fascicles were taken at two weekly intervals from randomly selected trees in all replicate plots. Needle dry mass per unit length was determined from measurements of total needle length and oven dry mass. Significant changes in needle dry mass per unit length over the growing season were linearly regressed against the number of days, t , after a reference starting date.

Allometric relationships

Trees were destructively sampled from both treatments during the winter periods of each year. The diameter and height of each tree was measured before it was extracted and divided into component parts. Roots were gently washed and carefully separated from soil. Tree components were then dried at 70°C until constant mass was reached, then weighed.

Allometric analysis was used to remove the influence of growth differences on allometry, so that the direct effects of treatment on allocation could be determined. The relationship between a particular component (y) and total biomass (x) was modelled using the following general linear model,

$$\log_e y = b_0 + b_1 \log_e x \quad (2.2)$$

Analysis of covariance was used to test if slopes (b_1) of fitted equations significantly differed between treatments. To determine the magnitude of treatment differences in

allometry, Equation 2.2 was separately fitted to data for each treatment. From these functions, a size adjusted comparison of allocation ratios was made between treatments at the end of the second year.

Seasonal changes in tree component biomass

Biomass prediction equations were developed by regressing weight of a particular component (y) against tree diameter (A_d ; mm tree⁻¹) and height (h_t ; mm tree⁻¹) using the following equation,

$$y = c_1(A_d)^{c_2}(h_t)^{c_3} \quad (2.3)$$

where c_1 , c_2 , and c_3 were determined (Table 2.1) using non-linear least squares regression. The weighted regression procedure in SAS (SAS Institute, 1996) was used to stabilise variance in the dependent variable and data was pooled by year as no significant differences in equation coefficients were detected.

Development of *Pinus radiata* foliage mass over the growing season was scaled using estimates of needle length. For the treatment without broom, this scaling included a correction to account for the seasonal increase in needle dry mass per unit length. Changes in branch and stem biomass were scaled throughout the year using the allometric relationship (Eq. 2.3, with coefficients in Table 2.1.).

Table 2.1. Parameters of the function (Eq. 2.3) used to predict component weights of *Pinus radiata* growing with and without broom. See text for explanation of symbols. The coefficient of determination (r^2), and level of significance is shown for all relationships. Asterisks *** represent significance at $P = 0.001$.

Treatment	Component weight	Parameter			r^2
		c_1	c_2	c_3	
With broom	Foliage	-	2.9967	-0.6693	0.96***
	Stem and branches	0.000862	1.9582	0.7887	0.98***
Without broom	Foliage	0.0158	1.7596	0.5136	0.98***
	Stem and branches	0.000104	2.1224	-	0.99***

Influence of broom competition for light and water on tree growth

A perennial problem encountered in competition studies is that treatment induced differences in initial tree size often bias relationships developed between availability of a particular resource (e.g., water) and tree growth (Bazazz, 2002). Further confounding may also occur if competition effects are studied at sub-annual periods as seasonal influences on conifer development are substantial. Following Kimberley and Richardson (2003), the confounding influences of initial tree size and season were removed by using the following modelling technique.

For trees in plots without broom, the underlying trend in biomass growth, G , was modelled using the simple power equation as,

$$G = d_1 t^{d_2} \quad (2.4)$$

where time is t and d_1 and d_2 are determined using a non-linear least squares regression procedure.

The seasonal influence on growth was modelled by superimposing the following single term Fourier series into Equation 2.4,

$$s(t) = \omega(\sin(2\pi(t + t_0 - t_m)) - \sin(2\pi(t_0 - t_m))) \quad (2.5)$$

where $s(t)$ is seasonally adjusted time, t_m is the time when growth reaches a maximum, ω is the amplitude of the seasonal effect, and t_0 is a reference starting point, when the series is constrained to equal 0 ($t_0 = 1$ January 2000).

Equation 2.5 was incorporated into the growth equation (Eq. 2.4) by using seasonally adjusted time, $t + s(t)$, in place of actual time, t , as,

$$G = d_1 (t + s(t))^{d_2} \quad (2.6)$$

Growth rate can be expressed as a function of initial tree size, G_i , by the derivative of Equation 2.6, which is,

$$\frac{dG}{dt} = (1 + 2\pi\omega \cos(2\pi(t + t_0 - t_m)))d_1^{(1/d_2)}d_2G_i^{(1-1/d_2)} \quad (2.7)$$

Biomass growth of *Pinus radiata* in plots without broom was modelled by Equation 2.6 using the non-linear least squares regression procedure. Using the coefficients obtained from this fit, predictions of biomass growth for *Pinus radiata* growing with broom were made at two monthly intervals throughout the experiment using Equation 2.7. The ratio of actual biomass growth to these predicted values was then calculated using data from individual plots. This ratio, termed fractional biomass growth, f_b , was regressed against average ψ_e using the following exponential function,

$$f_b = g_1 e^{-g_2(-\psi_e)} \quad (2.8)$$

where g_1 and g_2 are determined using a non-linear least squares regression procedure.

A simple index of shading was calculated as the product of average broom leaf area index, L_b , and mean relative height of the broom, h_r , (broom height/tree height). This index was included in the following non-linear model,

$$f_b = 1 - (1 - e^{-j_1(-\psi_e)})^{j_2} (j_3 e^{-j_4(L_b h_r)}) \quad (2.9)$$

with average ψ_e and the empirically determined parameters j_1 , j_2 , j_3 and j_4 to investigate if competition for light significantly influenced tree growth.

Data analysis

Data were subjected to a two way analysis of variance (ANOVA). Variables were tested for normality and homogeneity of variance and transformations made as necessary to meet the underlying statistical assumptions of ANOVA. All pairwise comparisons of individual means were undertaken by Students t-test. Differences were considered to be significant at $P < 0.05$.

RESULTS

Predawn needle water potential

The total amount and distribution of rainfall varied considerably between the two years of the study (Fig. 2.1). The annual precipitation of 648 mm over the first year was well below average, while the 910 mm which occurred during the second year was considerably above average for this study area. During the first year, only 28% of the annual total fell during summer and autumn and rainfall over the three month period from February to May was the lowest since records began in 1890 (Met Service database). In the second year 40% (375 mm) of the rainfall occurred during the very wet summer, and the remainder was evenly distributed throughout spring, autumn and winter (Fig. 2.1).

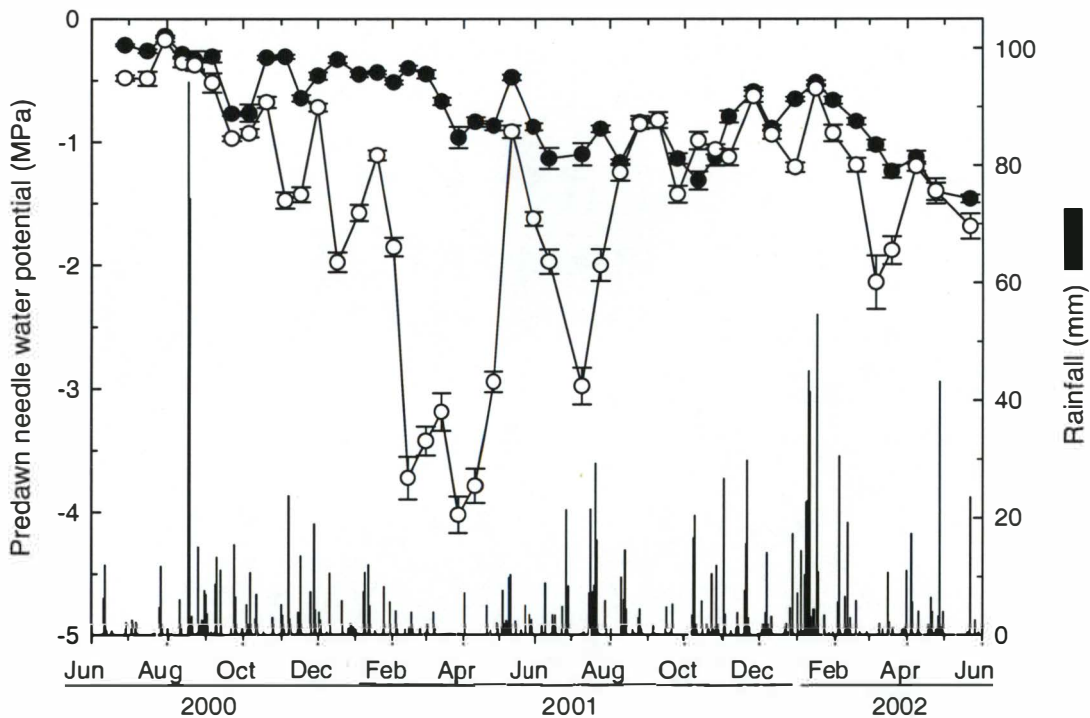


Figure 2.1. Distribution of precipitation from June 2000 - June 2002 (bars) and seasonal changes in predawn needle water potential of trees growing with broom (open symbols) and without broom (filled symbols). Each point shown is the mean \pm standard error of six plots.

Although the presence of broom induced consistently more negative values of ψ_e in *Pinus radiata*, treatment differences were more pronounced during the first year (Fig. 2.1). For trees growing without broom, ψ_e was high throughout the first year, never falling below -1 MPa. In contrast, ψ_e of trees growing with broom declined after mid-spring reaching lows of -4 MPa during the very dry autumn period before fully recovering after heavy rain in late winter. During the second year, ψ_e remained relatively high in both treatments over spring and summer. The only significant treatment divergence occurred during early autumn when ψ_e in the treatment with broom declined to -2.1 MPa.

Tree characteristics

Groundline diameter, height, basal area and crown diameter of *Pinus radiata* were all significantly influenced by treatment, age and their interaction (Table 2.2). At the end of the second year, trees growing without broom were two-fold taller and had a crown diameter four-fold greater than trees in plots with broom. However, basal area was the most sensitive indicator of competition. Treatment differences in basal area, which became significant ($P < 0.05$) one month after measurements started (winter 2000), increased from six-fold at the end of the first year to 12-fold at the end of the year two (Table 2.2).

Variation in the height to diameter ratio was attributable to both treatment, time and their interaction (Table 2.2). For trees in plots without broom values declined slightly during the first year (-15%), then stabilised. For trees in plots with broom the ratio of height to diameter increased 43% over the course of the trial, with the most marked changes occurring over year two (Table 2.2).

Dry matter partitioning

The ratios of component biomass to total biomass are shown in Table 2.3. At the start of the experiment, ratios were very similar and did not significantly differ in any category. Over the course of the experiment, allocation to stemwood significantly increased in the treatment with broom and significantly declined in the treatment without broom. Allocation to branches significantly increased in both treatments with time. This occurred at a significantly faster rate for trees growing with broom. Although allocation

to foliage declined with time, no significant treatment differences were detected. The proportion of dry matter allocated to roots was not significantly affected by time or treatment (Table 2.3).

Table 2.2. Characteristics of treatment plots during the first (June 2000, age 1) second (June 2001) and third (June 2002) winter periods after establishment for *Pinus radiata* growing with (B) and without broom (N). Each value is the mean \pm standard error from six sample plots. For each year and variable, students t-test was performed between treatments. Means followed by the same letter are not significantly different at $P < 0.05$. Asterisks *** represent significance at $P = 0.001$.

	Tree height (mm)	Root collar diameter (mm)	Basal area (mm ²)	Crown diameter (mm)	Ht : diam. ratio
<i>June 2000</i>					
B	537 (26) a	13.1 (0.6) a	141 (14) a	257 (15) a	41 (0.2) a
N	576 (18) a	14.7 (0.5) a	176 (12) a	295 (13) a	39 (0.6) b
<i>June 2001</i>					
B	919 (42) a	20.1 (0.9) a	333 (31) a	370 (19) a	46 (0.5) a
N	1670 (59) b	50.4 (1.6) b	2 072 (130) b	960 (26) b	34 (0.8) b
<i>June 2002</i>					
B	1 646 (112) a	27.9 (1.4) a	633 (65) a	483 (22) a	59 (1.7) a
N	3 265 (70) b	99.2 (2.7) b	7 766 (446) b	1877 (35) b	33 (0.6) b
<i>Significance of two-way repeated ANOVA</i>					
Treatment (T)	***	***	***	***	***
Year (Y)	***	***	***	***	***
T x Y	***	***	***	***	***

Allometric analysis (Table 2.4) provided a more accurate interpretation of treatment influences on allocation patterns than conventional analysis (Table 2.3). Compared with *Pinus radiata* in weed-free plots, trees growing with broom allocated dry matter preferentially to stems (+8%) at the expense of foliage (-4%), roots (-2%) and branches (-2%). Adjustment for plant size by allometric analysis substantially reduced treatment differences in stem (+14% vs +8%) and branch (-15% vs -2%) ratios found by conventional analysis, and altered the direction of treatment induced changes in foliage allocation (Table 2.4). Allometric analysis indicated that treatment did not significantly influence the proportion of dry matter allocated to roots (Table 2.4).

Table 2.3. Variations in the ratios of root, stem, branch and foliage mass to total dry mass during the first (June 2000, age 1) second (June 2001) and third (June 2002) winter periods after establishment, for *Pinus radiata* growing with (B) and without broom (N). Each value is the mean \pm standard error from at least seven trees. For each year and variable, students t-test was performed between treatments. Means followed by the same letter are not significantly different at $P < 0.05$. Asterisks *** represent significance at $P = 0.001$; ns = non-significant at $P = 0.05$.

	Root:Total	Stem:Total	Branches:Total	Foliage:Total
<i>June 2000</i>				
B	0.141 (0.008) a	0.367 (0.016) a	0.048 (0.012) a	0.444 (0.019) a
N	0.131 (0.009) a	0.364 (0.015) a	0.048 (0.008) a	0.457 (0.022) a
<i>June 2001</i>				
B	0.130 (0.010) a	0.362 (0.007) a	0.102 (0.009) a	0.406 (0.008) a
N	0.134 (0.014) a	0.309 (0.007) b	0.167 (0.016) b	0.390 (0.010) a
<i>June 2002</i>				
B	0.110 (0.009) a	0.406 (0.012) a	0.139 (0.008) a	0.345 (0.009) a
N	0.122 (0.006) a	0.263 (0.019) b	0.293 (0.027) b	0.322 (0.012) a
<i>Significance of two-way ANOVA</i>				
Treatment (T)	ns	***	***	ns
Year (Y)	ns	ns	***	***
T x Y	ns	***	***	ns

Table 2.4. Effects of treatment on the allometric relationship $\log_e y = b_0 + b_1 \log_e x$ between selected pairs (x , y) of dimensions from *Pinus radiata*. The F -values and significance levels from analysis of covariance are presented for the effects of treatment on the allometric coefficient b_1 . Also shown are the F -values and significance levels for the covariate (x). The treatment influence on allometry is expressed as the percentage difference in $y:x$ between treatments at the end of the experiment (June 2002), relative to trees growing without broom. For comparative purposes treatment differences obtained using conventional analysis are also shown. Asterisks *, *** represent significance at $P = 0.05$, and 0.001, respectively; ns = non-significant at $P = 0.05$.

$x - y$	Covariate	Treatment	Change in ratio $y:x$ (%)	
			Allometric	Conventional
$W_{total} - W_{root}$	2 637.4***	2.4 ^{ns}	-2	-1
$W_{total} - W_{stem}$	5 678.7***	12.7***	+8	+14
$W_{total} - W_{branch}$	1 424.0***	6.8*	-2	-15
$W_{total} - W_{foliage}$	7 801.9***	6.5*	-4	+2

Tree phenology

Needle extension started shortly after budburst, during early spring. Following an initial period of slow growth, the rate of elongation increased to a maximum (t_i) in both treatments during late spring (Table 2.5). By early autumn needles on trees growing with broom had reached 95% of their maximum length (t_{95}). Needle extension on trees growing without broom continued for a significantly longer time reaching t_{95} during late autumn (Table 2.5).

Variability in the maximum rate of extension (l_i) and total needle length (l_m) was attributable to both treatment and year (Table 2.5). Trees growing without broom developed longer needles (average $l_m = 112$ mm vs 45 mm) at a faster maximum rate (average $l_i = 0.85$ mm day⁻¹ vs 0.47 mm day⁻¹) than trees in plots with broom. Both l_m and l_i were significantly greater in the second year for trees growing with broom (Table 2.5).

Table 2.5. Maximum length, l_m , length growth rate at the point of inflexion, l_i , the time of inflexion, t_i , and the time taken for elongation to reach 95% of the total length, t_{95} , for current needles on trees growing in plots with (B) and without broom (N). The parameters were derived from von Bertalanffy equations used to model individual tree needle length in relation to the number of days since the start of spring. Each value is the mean \pm standard error from ten trees. For each year and variable, students t-test was performed between treatments. Means followed by the same letter are not significantly different at $P < 0.05$. Asterisks *, **, *** represent significance at $P = 0.05$, 0.01, and 0.001, respectively; ns = non-significant at $P = 0.05$.

	l_m (mm)	l_i (mm day ⁻¹)	t_i (day)	t_{95} (day)
<i>Year 1</i>				
B	36 (4) a	0.384 (0.049) a	79 (3) a	193 (10) a
N	107 (2) b	0.792 (0.027) b	85 (3) a	254 (7) b
<i>Year 2</i>				
B	54 (8) a	0.55 (0.042) a	81 (4) a	193 (13) a
N	117 (5) b	0.903 (0.064) b	72 (4) a	246 (16) b
<i>Significance of two-way ANOVA</i>				
Treatment (T)	***	***	ns	***
Year (Y)	*	**	ns	ns
T x Y	ns	ns	*	ns

Seasonal changes in tree biomass growth

The presence of broom significantly ($P < 0.0001$) reduced growth of component and above-ground biomass over the two year period (Table 2.6). Treatment differences in above-ground biomass significantly diverged over time from nine-fold at the end of the first year to 25-fold at the end of year two. Similar divergence was noted for component biomasses (Table 2.6).

Table 2.6. Accumulated component and above-ground biomass during the first (June 2000, age 1) second (June 2001) and third (June 2002) winter periods after establishment for *Pinus radiata* growing with (B) and without broom (N). Each value is the mean \pm standard error from six sample plots. For each year and variable, students t-test was performed between treatments. Means followed by the same letter are not significantly different at $P < 0.05$. Asterisks *** represent significance at $P = 0.001$.

	Woody biomass (g tree ⁻¹)	Foliage biomass (g tree ⁻¹)	Above-ground biomass (g tree ⁻¹)
<i>June 2000</i>			
B	20.5 (2.7) a	33.9 (3.8) a	54.4 (6.6) a
N	19.8 (2.0) a	47.2 (3.5) b	67.0 (5.5) a
<i>June 2001</i>			
B	71.4 (8.9) a	85.2 (9.2) a	156.6 (18.1) a
N	757.3 (74.6) b	718.6 (51.9) b	1475.9 (126.5) b
<i>June 2002</i>			
B	207.5 (29.2) a	154.0 (16.5) a	361.5 (45.6) a
N	5 909.7 (461.5) b	3 297.8 (191.3) b	9 207.5 (652.4) b
<i>Significance of two-way repeated ANOVA</i>			
Treatment (T)	***	***	***
Year (Y)	***	***	***
T x Y	***	***	***

In the treatment without broom, total biomass increased exponentially over time (Fig. 2.2b). Seasonal fluctuations in biomass growth exhibited a regular pattern during both years, with maxima occurring in early summer (t_m = December 19) and minima during winter. The equation used (Eq. 2.6) to model total biomass of *Pinus radiata* growing without broom (Fig. 2.2b) fitted the data very well ($r^2 = 0.999$; $P < 0.0001$). All

coefficients were highly significant ($P < 0.0001$) and estimated values for ω , t_m , d_1 and d_2 were 0.129, 0.969, 1293, and 2.807, respectively.

Seasonal growth patterns were less consistent between years for trees growing with broom (Fig. 2.2a). During the first year, biomass increment reached a seasonal maximum during mid-spring after which time growth slowed, virtually ceasing after late summer. Although biomass growth during the second year also reached maximum rates in late spring, increment continued throughout the summer and autumn period (Fig. 2.2a).

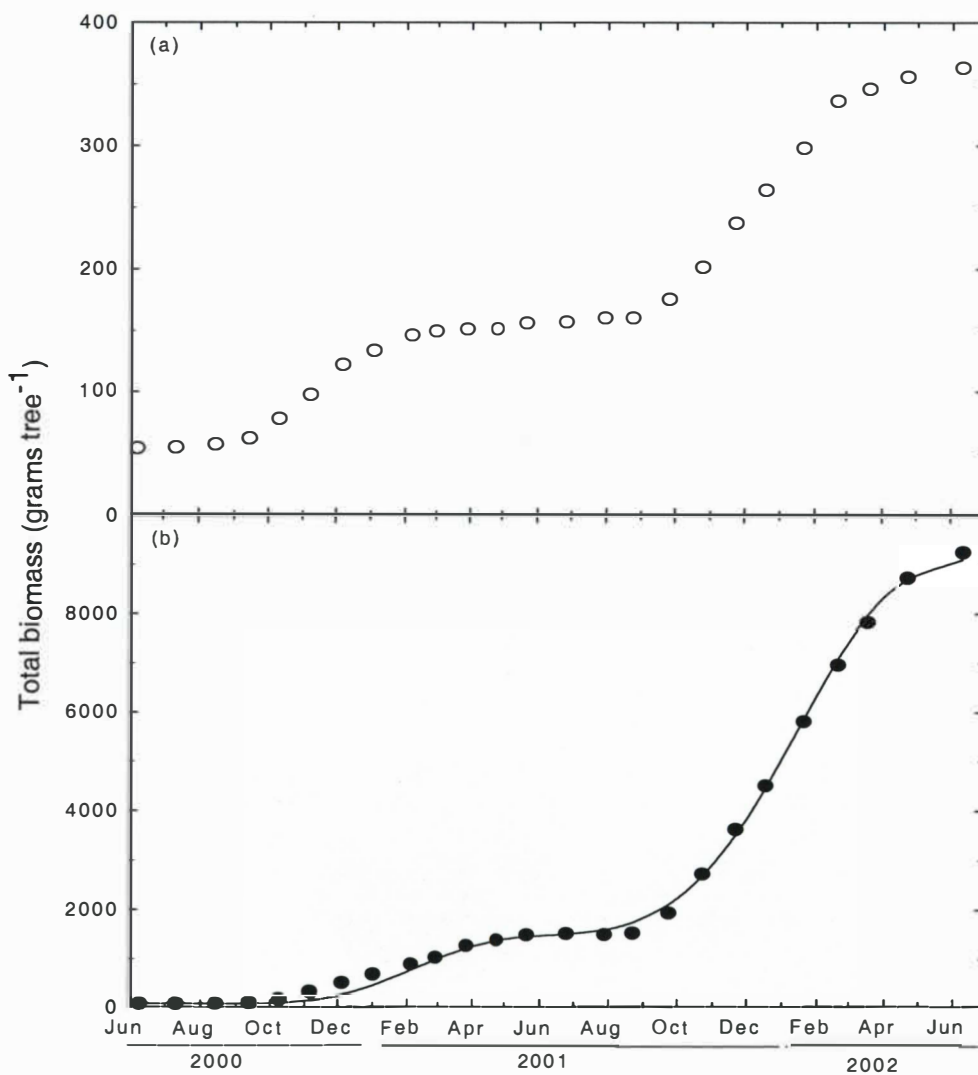


Figure 2.2. Seasonal changes in above-ground biomass for (a) trees growing with broom (open symbols) and (b) without broom (filled symbols). The solid line in figure (b) shows modelled above-ground biomass growth. Note differences in scale on y-axis.

Broom growth

Broom leaf area index increased exponentially over time, from average values of $0.76 \text{ m}^2 \text{ m}^{-2}$ in year 1 to $2.26 \text{ m}^2 \text{ m}^{-2}$ during year 2 (Fig. 2.3a). During both years, L_b followed a regular seasonal pattern, reaching annual maxima during late summer, before steadily declining over autumn as a result of leaf loss (Fig. 2.3a). The rate and pattern of height growth was very similar for broom and *Pinus radiata* growing in the same treatment plots (Fig. 2.3b). For both species, height growth commenced in early spring. Maximum rates of growth were reached in early summer, after which time growth declined, virtually ceasing by early autumn onwards.

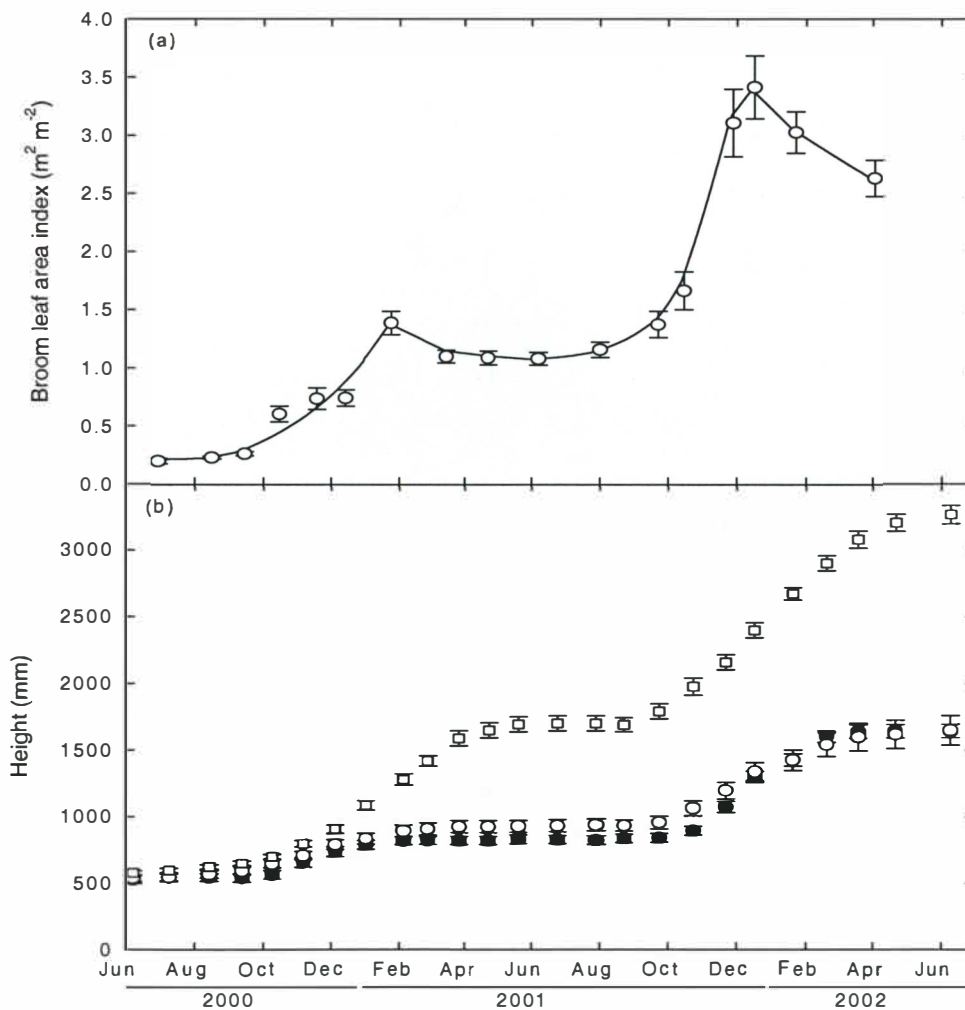


Figure 2.3. Seasonal changes in (a) measured (open circles) and modelled (solid line) broom leaf area index and (b) height of broom (filled circles) and *Pinus radiata* growing with (open circles), and without broom (open squares). Each value shown is the mean \pm standard error of 6 sample plots.

Mechanisms of competition by broom

Fractional biomass growth (f_b) was significantly and strongly correlated ($r^2 = 0.81$) to ψ_e (Table 2.7). Over comparable values of ψ_e , fractional biomass growth was significantly lower during the second year (Figure 2.4, Table 2.7). These annual differences, which were most pronounced at high values of ψ_e (< 1 MPa), were, on average, 15% lower over the range of ψ_e (Table 2.7).

Table 2.7. Statistics of models used to predict fractional biomass growth of trees in plots with broom. The terms in these two models include average two monthly predawn needle water potential (ψ_e), broom leaf area index (L_b), and mean relative height of the broom (h_r). For both models parameter values, F -values, significance levels and residual sums of squares (RSS) are shown. Also shown are the percentage differences in model residual values between years 1 and 2, expressed relative to year 1. Residual values obtained from each model were tested for significant differences between years. Asterisks *** represent significance at $P = 0.001$, ns = non-significant at $P = 0.05$.

	Model terms	
	ψ_e	$\psi_e, (L_b, h_r)$
Parameter		
g_1	1.81	-
g_2	1.73	-
j_1	-	1.62
j_2	-	2.94
j_3	-	1.18
j_4	-	0.40
Model statistics		
F -value	300.15	384.93
P	< 0.0001	< 0.0001
RSS	1.0183	0.4335
Annual diff. residuals (%)	-15***	-4 ^{ns}

Addition of the shading index (L_b, h_r) to ψ_e accounted for almost all of the annual difference in fractional biomass growth (Table 2.7) and significantly improved the overall model, reducing the residual sums of squares by 57% (Table 2.7). The functional form of the modifier for light (Eq. 2.9) indicated that fractional biomass growth declined exponentially with increases in the shading index. Inclusion of the shading index and ψ_e

explained 92% of the variation in fractional biomass growth, and no significant collinearity was noted between these independent variables.

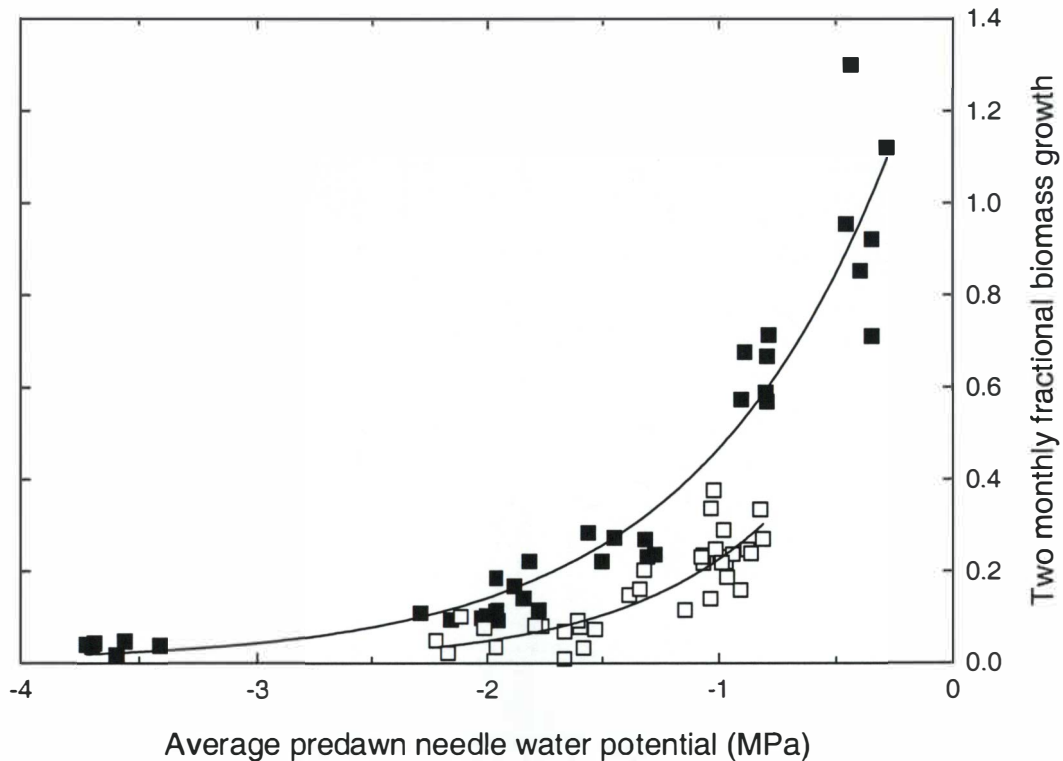


Figure 2.4. Relationship between average two monthly predawn needle water potential and fractional biomass growth of *Pinus radiata* growing in plots with broom over the first (filled squares) and second (open squares) years. Data shown are six plots, measured at six times over each of the two years ($n = 72$). The lines were fitted using the function, $f_b = g_1 e^{-g_2(-\psi_e)}$, where the parameter g_1 is 1.535 (year 1) and 1.19 (year 2) and parameter g_2 is 1.055 (year 1) and 1.54 (year 2).

DISCUSSION

The presence of broom retarded above-ground biomass growth of *Pinus radiata* by 25-fold over the studied two year period. Although it is known that broom reduces *Pinus radiata* volume growth on dryland sites (Richardson *et al.*, 1997), reductions of this magnitude have not been previously reported. These very pronounced treatment differences may have been caused by the drought prone nature of the soil, which has a comparatively low storage capacity.

During the first year, the strong link between ψ_e and fractional biomass growth for trees in plots with broom ($r^2 = 0.91$, Fig. 2.4) suggests growth losses were almost entirely attributable to water stress. By early summer, the presence of broom had induced high levels of water stress (-2 MPa) in *Pinus radiata* foliage, which resulted in growth losses of 90% (Fig. 2.4). As rainfall was very sparse after this time, ψ_e fell even further reaching lows of -4 MPa in late autumn (Fig. 2.1). In response to this severe water stress, biomass growth virtually ceased from mid-summer to late autumn (Fig. 2.2a).

The influence of broom on tree growth during the second year was mediated through light and water availability. Although ψ_e was strongly related to fractional biomass growth in the second year ($r^2 = 0.71$), values were on average 15% lower than in the first year (Fig. 2.4, Table 2.7). Inclusion of the shading index largely explained this difference, indicating competition for light by broom had a significant influence on tree growth over this period. This is not surprising, given that average L_b tripled from year 1 to year 2 (Fig. 2.3a). Numerous studies in wet areas have documented the detrimental influence of shading by weeds on conifer growth (Brand, 1986; Comeau, *et al.*, 1993; Richardson *et al.*, 1999).

The relative importance of weed competition for light and water will depend on both rainfall and root-zone water storage. Although rainfall was higher than average over the second year, seasonal water deficits still occurred in the treatment with broom as high transpiration from the broom often exceeded the low soil water storage of this shallow soil (0.3 m). In contrast, on wet sites in the Central North Island transpiration from broom is less likely to induce growth limiting seasonal water deficits as the soil has a high water storage. As a result tree growth in this region is mediated primarily through weed competition for light.

Increased allocation to stemwood for trees in plots with broom was accompanied by a significant increase in the height to diameter ratio (Table 2.2). These allometric changes allowed trees in this treatment to closely match height growth of the broom, over the two year period (Fig. 2.3b). Although water stress has been found to increase apical dominance (Pereira and Chaves, 1993), the most probable cause of this alteration to allometry was shading from the broom. This finding is consistent with studies in Scots pine (*Pinus sylvestris* L.) where greater interspecific competition has also been found to

increase stemwood allocation and the height to diameter ratio (Albrekston and Valinger, 1985; Nilsson and Albrekston, 1993; Vanninen and Mäkelä, 2000). The results from this study also confirm derivations based on the pipe model theory which predict a greater investment in stemwood of shaded trees (Mäkelä, 1986; Bartelink, 1998). From a physiological standpoint, increased height growth is likely to increase carbon assimilation, through minimising shading of the tree foliage by competing plants.

An increase in the root to shoot ratio, attributable mainly to a reduction in shoot growth rate, has often been observed when water is limiting (Ryan *et al.*, 1996). In this study, the presence of broom did not significantly alter partitioning to the roots. It is possible that the opposing influences of competition for light and water maintained this allometric equilibrium. However, this seems unlikely as treatment differences were not detected at the end of the first year, during which time water stress was by far the dominant influence on tree growth. Studies on young water stressed *Eucalyptus globulus* (Osório *et al.*, 1998) and juvenile *Pseudotsuga menziesii* trees subject to a wide range of competition (Newton and Cole, 1991) have also demonstrated low phenotypic plasticity in the root to shoot ratio.

Treatment induced differences in tree size have been found to bias most studies of competition to some degree (Bazzaz, 2002). In this experiment, competitive influences of broom on tree growth were effectively separated from the confounding effects of initial tree size and season, by incorporating these influences into the model. Use of this technique assumes tree growth in weed-free plots was not constrained by water availability. This assumption is supported by the very regular pattern of biomass growth exhibited by trees in this treatment, suggesting growth was limited by seasonal changes in temperature and light, rather than root-zone water content. In addition, measurements of ψ_e taken from these trees showed that water stress was relatively low, even during periods of severe drought. Other studies on dryland sites have also reported that water stress does not seriously limit growth of *Pinus radiata* in weed-free plots over the first three years following establishment (Sands and Nambiar, 1984; Richardson *et al.*, 1997).

When allometric analysis was applied, it becomes evident that many of the large differences observed at the end of the experiment reflect size dependent shifts in allocation patterns, rather than treatment differences. These results reinforce the findings

of several other researchers (Ledig *et al.*, 1970; Gebauer *et al.*, 1996; Osório *et al.*, 1998), that size dependent changes in allocation need to be separated from functional adjustments made in response to treatment.

In conclusion, severe water stress induced by broom did not significantly alter the root to shoot ratio in *Pinus radiata*. However, competition by broom for light did result in significant increases in stemwood allocation, which confirms derivations based on pipe model theory. Competition induced losses in tree above-ground biomass growth were almost entirely attributable to water stress during the first year. Broom restricted tree growth during the second year through competition for both light and water. This study highlights the importance of correcting for tree size when investigating the effect of weed competition on tree growth and allocation.

CHAPTER THREE

ABOVE-GROUND BIOMASS ACCUMULATION AND NITROGEN FIXATION OF BROOM (*CYTISUS SCOPARIUS* L.) GROWING WITH JUVENILE *PINUS RADIATA* ON A DRYLAND SITE².

INTRODUCTION

Broom (*Cytisus scoparius* L.) is a common introduced shrub within New Zealand which has colonised a wide range of habitats. As broom originates from the Mediterranean (Hegi, 1926) it has a number of dry climate adaptations including small deciduous leaves and a stem which is able to photosynthesise (Peterson and Prasad, 1998). These attributes and the ability of broom to fix nitrogen, grow rapidly and set large quantities of seed make it a very successful pioneer of open habitats, including those that experience soil water deficit, or are deficient in nitrogen (Williams, 1981).

As broom is able to photosynthesise at air temperatures as low as 4°C (Nilsen *et al.*, 1993) it can grow almost all year round on sites which are wet and have a mild winter (Fogarty and Facelli, 1999). The shrub is shade intolerant, prefers soils with moderate levels of nitrogen (Peterson and Prasad, 1998) and reaches optimum growth rates on fresh alluvium and recent soils with a high level of inorganic phosphorus (Williams, 1981). Although broom is classed as a drought tolerator (Bannister, 1986) little is known about how water deficit influences seasonal patterns of biomass accumulation.

Broom is widespread throughout the New Zealand plantation forestry estate (Richardson, 1993) where it competes vigorously with newly planted conifer seedlings. On sites where water is not limiting the presence of broom has been found to reduce volume growth in juvenile *Pinus radiata* by intercepting incident above-canopy radiation (Richardson *et al.*, 1996). Reductions in juvenile *Pinus radiata* volume growth have also been reported on dryland sites (Richardson *et al.*, 1997; Watt *et al.*, 2003) where the

² This chapter is in press with *Forest Ecology and Management* as Watt, M.S., Clinton, P.W., Whitehead, D., Richardson, B., Mason, E.G., and Leckie, A.C.

inducement of seasonal water deficit by broom was found to be the main mechanism of resource competition (Watt *et al.*, 2003).

As long term weed control studies are relatively rare, the influence of broom on conifer growth after the juvenile stage is poorly understood. After closure of the tree canopy broom will die out. As a large quantity of nitrogen is held in the stem, the decomposition of woody material after canopy closure may enhance tree growth. The likelihood of this occurring will depend on the extent to which broom competes for site resources after it is overtopped by the conifer, the nitrogen status of the site, and the rates of nitrogen transfer from the broom to the conifer.

Despite the widespread occurrence of broom in plantation forests, little research has investigated rates of nitrogen fixation. Nitrogenase activity in this species reaches optimum rates at 25°C and has been found to occur at temperatures as low as 2°C (Wheeler *et al.*, 1979). The onset of flowering reduces nitrogenase activity and rates also fall during drought periods in response to soil water deficit (Wheeler *et al.*, 1987). Compared to other nitrogen fixing species broom is not heavily nodulated (Helgersson *et al.*, 1984). Despite this effective nitrogen fixation has been documented in this species on sand soils in England, where accretion of nitrogen in the soil and biomass was found to be similar to that of other woody nitrogen fixing perennials (Dancer *et al.*, 1977).

An experiment on the Canterbury plains, New Zealand, was established to (i) quantify seasonal above-ground biomass increment and nitrogen sequestration by *Pinus radiata* and broom at a dryland site (ii) investigate how severe water deficit influences seasonal biomass accumulation of broom (iii) estimate annual nitrogen fixation by broom, and the extent of fixed nitrogen transfer to *Pinus radiata* using the natural ¹⁵N abundance technique (Shearer and Kohl, 1988). In light of these results the likely influence of broom on conifer growth after canopy closure is discussed.

METHODS

Site description

Measurements were taken over a one year period beginning June 2000, on an experiment located near Hororata, 60 km west of Christchurch, New Zealand (latitude

43° 34' S, longitude 171° 55' E, 210 m asl). The soil on the site, which is classified as a stony Lismore silt loam, is shallow, free draining and of low fertility (Kear *et al.*, 1967). Water storage capacity within the very stony soil (21% by volume) is limited to approximately 70 mm in the main rooting zone (0.3 m soil depth). At depths lower than 0.3 m, volumetric stone content increases to over 50%, and root density is very low. Seasonal water deficits are characteristic of this soil and very common near Hororata as long term average rainfall is relatively low (797 mm yr⁻¹) and evaporative demand over spring and summer high.

Experimental design and environmental measurements

Experimental plots were located within a 20 ha *Pinus radiata* plantation established during winter 1999, at a spacing of 4 x 2 m (1 250 stems ha⁻¹). During the summer of 1999 twelve plots were established in areas where natural broom regeneration was high. The twelve plots were divided into six blocks. Plots within each block were randomly assigned to two treatments, which included no control of broom and complete removal of all broom. Each plot was approximately 12 x 24 m and included an interior 24 measurement trees, completely surrounded by buffer rows of seedlings.

Weed control was achieved by applying 6.25 kg of terbuthylazine mixed with 900 g of clopyralid and 300 g of haloxyfop in 250 l ha⁻¹ of water. This herbicide was applied to designated plots to eliminate existing vegetation, which consisted almost entirely of broom. After spraying, any weed regrowth was removed by a combination of hand weeding and spot herbicide application.

Meteorological sensors were installed on a 3 m tower, located in a small clearing adjacent to the experimental plots. Hourly measurements of photosynthetically active photon flux density, air temperature and relative humidity were made above the canopy. In treatment plots adjacent to the tower a tipping bucket raingauge on a 1.5 m stand measured above-canopy rainfall. Soil temperature was measured in each treatment at a depth of 50 mm using thermocouple. Root-zone water storage in both treatments was recorded by two (one per treatment) time domain reflectometry sensors (Aquaflex, model SI. 60, Streat Instruments, Lincoln, New Zealand) installed within the tree rows, at a depth of 0.2 m.

Root-zone water storage on day i (W_i) was successfully modelled in both treatments by Watt *et al.* (2003) using the following water balance equation,

$$W_i = W_{i-1} + P_i - E_{ti} - E_{twi} - E_{bi} - E_{bwi} - E_{gi} - F_i \quad (3.1)$$

where P_i is rainfall, E_{ti} is transpiration from the dry tree canopy, E_{twi} evaporation from the wet tree canopy, E_{bi} transpiration from the dry broom canopy, E_{bwi} evaporation from the wet broom canopy, E_{gi} evaporation from the soil, and F_i drainage from the root zone. Each component in Equation 3.1 was estimated from field measurements and meteorological data collected at the experimental site. Independent measurements of W_i obtained from the soil water sensors were used to validate modelled values.

Seasonal changes in above-ground biomass of broom and Pinus radiata

At monthly intervals, leaf area index of the broom, L_b , was directly measured using a canopy analyser (LAI-2000, Li-Cor Inc., Lincoln, NE, USA). The plots were stratified into between and within row components as the influence of a strip herbicide applied after planting was still apparent. L_b was measured at 24 locations selected randomly within each component, and these plot level estimates were modelled against time using a segmented regression procedure (Hunt, 1982). Seasonal estimates of L_b for the entire plot were obtained by averaging modelled values for both components.

Linear allometric relationships ($y = uL_b$) between above-ground broom components ($g\ m^2$) and leaf area index, L_b , ($m^2\ m^{-2}$) were developed from five samples taken over a one year period from late spring 2000 (Table 3.1). In each sample, L_b within a square metre quadrat was measured, prior to harvesting of the plant material. Component weight ratios were determined by separating leaves from stems on three subsamples, which, together with the main sample, were then dried to constant mass and weighed. Seasonal changes in broom biomass were scaled throughout the year using these allometric relationships, parameterised from monthly estimates of L_b .

Groundline stem diameter and total height of each tree was recorded at monthly intervals. Prediction equations for *Pinus radiata* above-ground component mass were established by destructively sampling 40 trees at the start and end of the experiment. The

diameter and height of each tree was measured before it was harvested and divided into component parts (branches, stem and foliage). Component mass was regressed against tree diameter (A_d ; mm tree⁻¹) and height (h_t ; mm tree⁻¹) using the following function,

$$Y = v_1 A_d^{v_2} h_t^{v_3} \quad (3.2)$$

where the parameters v_1 , v_2 , and v_3 were empirically determined (Table 3.1) using non-linear least squares regression. The weighted regression procedure in SAS (SAS Institute, 1996) was used to stabilise variance in the dependent variable and data was pooled by treatment and year as no significant differences in equation coefficients were detected.

Table 3.1. Parameters of the functions used to predict component mass of *Pinus radiata* and broom. See text for explanation of symbols. The coefficient of determination (r^2), and level of significance is shown for all relationships. Asterisks *** represent significance at $P = 0.001$.

Species	Component	Parameter				r^2
		u	v_1	v_2	v_3	
<i>Pinus radiata</i>	Foliage	-	-	2.728	-0.555	0.99***
	Stem and branches	-	2.34E-3	1.932	-	0.99***
Broom	Foliage	44.7	-	-	-	0.93***
	Stem and branches	327.9	-	-	-	0.93***

Development of *Pinus radiata* foliage mass over the growing season was scaled by non-destructive measurements of current needle length, using the methodology described in Chapter Two. For the treatment without broom this scaling included a correction to account for the seasonal increase in needle dry mass per unit length. Changes in branch and stem biomass were scaled throughout the year using the allometric relationship (Equation 3.2, with coefficients in Table 3.1).

Sampling for seasonal changes in natural ¹⁵N abundance

Destructive harvests of *Pinus radiata* needles were taken over the course of the year during mid-winter (2000), early spring, late spring, mid-summer, early autumn, late

autumn and mid-winter (2001). In each of the six replicate plots, the youngest fully expanded foliage from three to five randomly selected trees was sampled, and bulked. From the 40 trees destructively sampled over the winter periods of 2000 and 2001, woody tissues from the 24 trees (6 for each treatment in each year) nearest to the treatment plots were analysed for $\delta^{15}\text{N}$.

Broom above-ground components were sampled at the same time as the *Pinus radiata* foliage, over the course of the year. In each plot with broom, three current apical shoots with attached leaves, were harvested from randomly selected plants. Samples were separated into leaves and stems and bulked by plot.

Determination of symbiotic nitrogen fixation in the absence of non-atmospheric nitrogen source.

Broom seedlings were grown for five months in a naturally lit glasshouse to determine the $\delta^{15}\text{N}$ value (*B*) of the plants growing under fully symbiotic conditions. Prior to planting, 14 plastic pots of 4 l capacity were filled with sterilised nitrogen free sand. During late autumn 2001, each pot was planted with three nodulated cotyledon seedlings, removed from the experimental site. After establishment, seedlings were thinned down to a single plant per pot. Seedlings were watered at two day intervals, with a nitrogen free solution (Virginia and Delwiche, 1982), so that the sand within the pot was maintained at a level close to field capacity.

All seedlings were harvested in mid-spring 2001. Seedlings were separated into above-ground stem and leaves, and bulked over two pots, to give a total of seven samples per plant component.

Estimation of nitrogen fixation

Plant samples collected from the field and glasshouse were oven dried at 70°C until constant mass was reached, then weighed. Woody tissue was initially ground to < 1 mm using a Wiley mill (Model 4, Arthur H. Thomas Company, Phil, PA, USA). All samples were then milled to a fine powder using a ring grinder (Rocklabs, Auckland, New Zealand). Subsamples of plant tissues were analysed for nitrogen concentration, [N],

and $\delta^{15}\text{N}$ abundance by Waikato Stable Isotope Unit using continuous-flow mass spectrometry (Europa Scientific 20/20 isotope analyser).

Nitrogen isotope composition was expressed as,

$$\delta^{15}\text{N} = 1000 \times \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \quad (3.3)$$

where the standard is atmospheric nitrogen (0.3663 atom % ^{15}N).

Isotopic mass balance of above-ground tissues ($\delta^{15}\text{N}_{\text{ag}}$) was calculated as,

$$\delta^{15}\text{N}_{\text{ag}} = \frac{[(\delta^{15}\text{N}_{(\text{stems})} \times \text{mass N in stems}) + (\delta^{15}\text{N}_{(\text{leaves})} \times \text{mass N in leaves})]}{(\text{mass N in above-ground tissues})} \quad (3.4)$$

The percent of nitrogen derived from the atmosphere (%Ndfa) for field grown broom was calculated as,

$$\% \text{Ndfa} = ([\delta^{15}\text{N}_{\text{ref}} - \delta^{15}\text{N}_{\text{fix}}] / [\delta^{15}\text{N}_{\text{ref}} - B]) \times 100 \quad (3.5)$$

where $\delta^{15}\text{N}_{\text{ref}}$ is the $\delta^{15}\text{N}$ value of the reference *Pinus radiata* growing without broom, $\delta^{15}\text{N}_{\text{fix}}$ is the $\delta^{15}\text{N}$ value of the field grown broom and B is the $\delta^{15}\text{N}$ value of broom grown in nitrogen free sand. Estimates of annual fixation for the broom used weighted %Ndfa calculated from above-ground samples of both *Pinus radiata* and broom. However as it was not practical to repeatedly sample *Pinus radiata* woody tissues, seasonal values of %Ndfa for the broom were calculated from tree foliage samples.

Total nitrogen fixed by the broom was calculated by,

$$\text{Total N fixed} = [\% \text{Ndfa} / 100] \times \text{mass N in above-ground tissues} \quad (3.6)$$

where %Ndfa represents the weighted average for above-ground broom.

Statistical analyses

Two way analysis of variance was conducted using SAS (SAS Institute, 1996) to test for the main and interactive effects of time and species on $\delta^{15}\text{N}$. Standard errors for %Ndfa were calculated by propagating the errors in all terms of Equation 3.5 using the formula described by Beers (1957). A t-test was then used to determine if %Ndfa differed significantly between the winter periods of 2000 and 2001.

RESULTS

Above-ground seasonal biomass accumulation and nitrogen uptake

Broom above-ground biomass increased five-fold over the course of the year (Fig. 3.1a). From starting values of 773 kg ha⁻¹ biomass increased exponentially over spring and early summer reaching a seasonal maximum of 5 519 kg ha⁻¹ in mid-summer. Above-ground biomass of the broom declined from late summer to 4 250 kg ha⁻¹ during late autumn as a result of leaf loss over this very dry period (Fig. 3.1a).

Treatment differences in *Pinus radiata* above-ground biomass, which became significant from mid-winter onwards diverged markedly after mid-spring (Fig 3.1b). In plots without broom biomass of the *Pinus radiata* increased 22-fold over the course of the year to final weights of 1 869 kg ha⁻¹. Biomass increment in this treatment reached maximum rates during early summer and did not start to decline until early winter. In contrast, biomass of *Pinus radiata* growing in plots with broom increased only three-fold over the course of the growing season to values of 192 kg ha⁻¹. Maximum rates of growth were reached in mid-spring after which time growth rapidly declined, virtually ceasing from late summer onwards (Fig. 3.1b).

As the nitrogen concentration, [N], of above-ground broom tissues remained relatively constant at 35 mg g⁻¹ relative annual rates of nitrogen sequestration were similar to biomass growth increasing five-fold to 142 kg ha⁻¹ in late autumn. Above-ground [N] of *Pinus radiata* in both treatments declined to 10 mg g⁻¹ at the end of the growing season from starting values of 17 mg g⁻¹ for trees in plots without broom and 14 mg g⁻¹ for trees in plots with broom. Nitrogen uptake increased 13-fold for trees in plots without broom to 18.7 kg ha⁻¹, and two-fold for trees in plots with broom to 2.1 kg ha⁻¹.

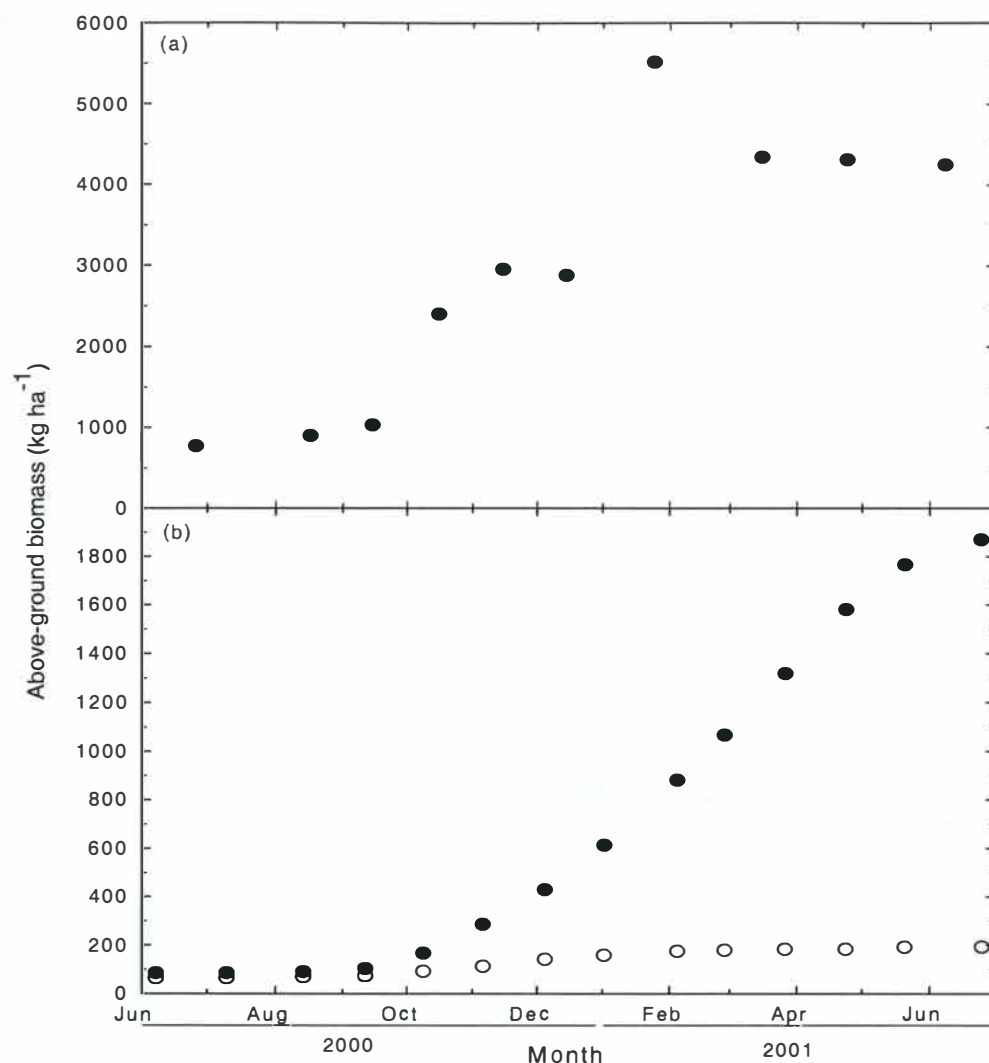


Figure 3.1. Estimated seasonal changes in above-ground biomass for (a) broom and (b) *Pinus radiata* growing with (open circles) and without (filled circles) broom. Note differences in scale on y-axis.

$\delta^{15}\text{N}$ values and %Ndfa for broom.

When averaged across the growing season there were significant differences in $\delta^{15}\text{N}$ values between species and treatments (Fig. 3.2). The highest $\delta^{15}\text{N}$ values were recorded for trees growing without broom, intermediate $\delta^{15}\text{N}$ values were recorded for trees growing with broom, and the lowest $\delta^{15}\text{N}$ values occurred in broom (Fig. 3.2). The above-ground $\delta^{15}\text{N}$ value of fixed nitrogen obtained from broom grown in nitrogen-free

sand (-0.63 ‰) was lower than above-ground $\delta^{15}\text{N}$ values for field grown broom.

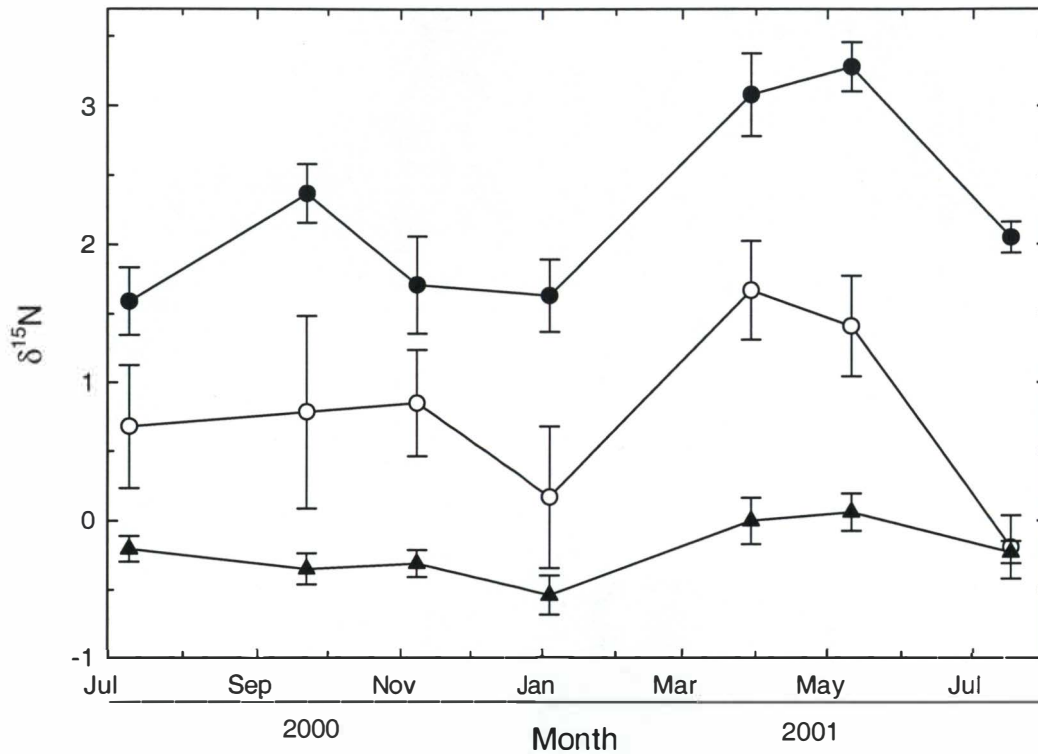


Figure 3.2. Seasonal changes in $\delta^{15}\text{N}$ for foliage of *Pinus radiata* growing with broom (open circles) and without broom (filled circles), and broom above-ground tissues sampled from plants grown in the field (filled triangles). Each point shown is the mean \pm standard error of six sample plots.

Seasonal changes in $\delta^{15}\text{N}$ were significant for trees growing without broom ($P < 0.0001$) and in field grown broom ($P = 0.0168$). However as fluctuations in $\delta^{15}\text{N}$ over the growing season followed a similar trend (Fig. 3.2) the interaction between time and species was insignificant.

Although %Ndfa of the broom increased with soil temperature to a seasonal maximum of 95% during mid-summer, there was a temporary depression in values around late spring, which occurred shortly after broom flowering (Fig. 3.3). The decline in %Ndfa after mid-summer coincided with a period of very low soil water storage after which time almost all of the broom foliage had been shed. Values remained low over the winter period during which time temperatures reached the seasonal minimum (Fig. 3.3).

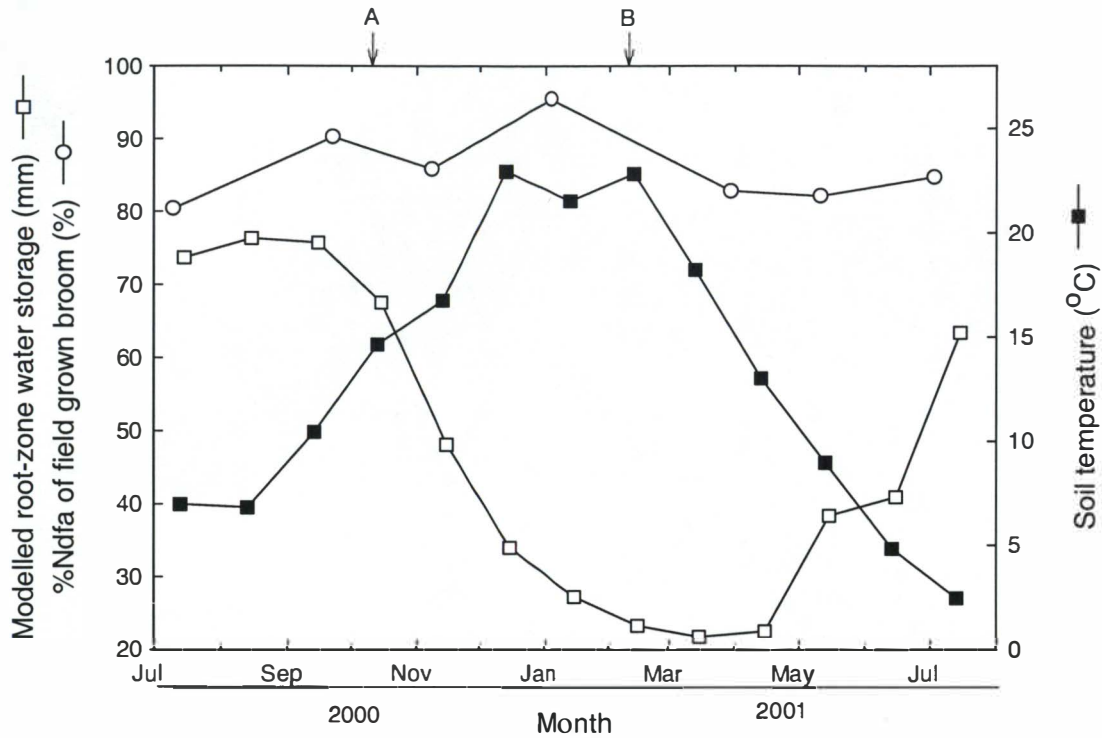


Figure 3.3. Seasonal changes in broom %Ndfa (open circles), soil temperature (filled squares) and modelled root-zone water storage (open squares), from Watt *et al.* (2003). Arrows (A) and (B) indicate the onset of flowering and leaf fall, respectively.

Broom derived a high proportion of above-ground nitrogen from the atmosphere. Estimates of %Ndfa made from above-ground tissues of both broom and the reference *Pinus radiata*, indicated an insignificant increase from 78% at the start to 84% at the end of the growing season (Table 3.2).

Table 3.2. Estimates of %Ndfa in field grown broom. Also shown are the above-ground $\delta^{15}\text{N}$ values for *Pinus radiata* and broom which were to calculate %Ndfa (see text for explanation of symbols). The standard errors shown for $\delta^{15}\text{N}$ values are calculated from six samples, and standard errors for %Ndfa are calculated from the components of Equation 3.5, using the formula described by Beers (1957).

Date	$\delta^{15}\text{N}_{\text{ref}}$	$\delta^{15}\text{N}_{\text{fix}}$	B	%Nd _{fa}
	‰			
Winter 2000	1.38 (0.31)	-0.20 (0.09)	-0.64 (0.08)	78 (6)
Winter 2001	1.84 (0.20)	-0.24 (0.07)	-0.64 (0.08)	84 (4)

Using these estimates, annual fixation by the broom was calculated to be $94 \text{ kg N}^{-1} \text{ ha}^{-1}$. Assuming an average %Ndfa of 81% for the entire year, broom fixed $111 \text{ kg N}^{-1} \text{ ha}^{-1}$ into above-ground tissues between winter and early autumn, and returned $17 \text{ kg N}^{-1} \text{ ha}^{-1}$ to the soil as leaf litterfall from mid to late autumn (Fig. 3.4).

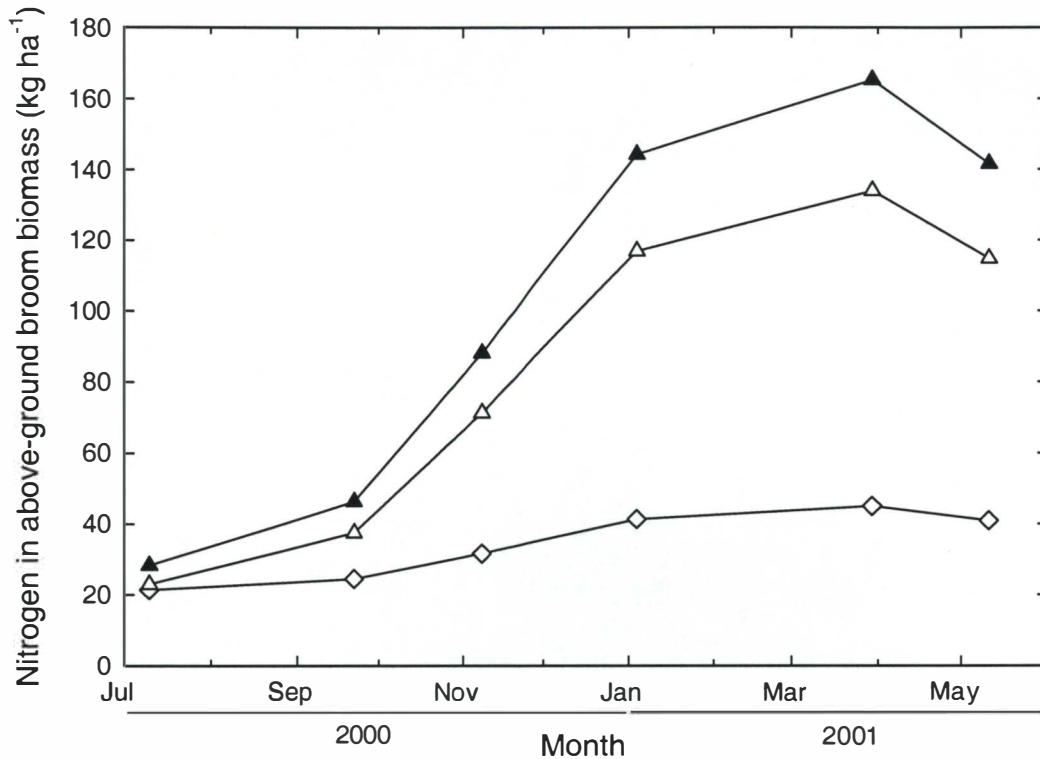


Figure 3.4. Cumulative above-ground nitrogen uptake (filled triangles), uptake from fixation (open triangles), and uptake from the soil (open diamonds) for broom. Uptake of nitrogen from fixation was calculated assuming an average %Ndfa of 81% throughout the course of the growing season, and soil nitrogen uptake was calculated as the difference between total nitrogen and fixed nitrogen.

DISCUSSION

*Annual nitrogen fixation and nitrogen transfer to *Pinus radiata**

During the second year of growth, broom fixed a substantial amount of nitrogen ($111 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) into above-ground tissues. Although these estimates do not include nitrogen fixed below-ground, it is likely that contributions from this source are low. Measurements taken at the end of the growing season indicate roots constituted only 12%

of total broom biomass. If [N] values found for broom grown in the nitrogen free medium are applied to these root masses, contributions from this source only increase annual estimates of total sequestration by 6% ($9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$).

These estimates of annual fixation are considerably higher than values reported for juvenile broom elsewhere in the literature which range from 10 to 36 kg N ha^{-1} for above-ground plant parts (Wheeler *et al.*, 1987; Dancer *et al.*, 1977). This difference may be due to previous use of the acetylene reduction assay technique which has been found to severely underestimate nitrogen fixation (Sprent and Minchin, 1985).

The intermediate values of $\delta^{15}\text{N}$ found for trees growing with broom (Fig. 3.2) suggest that there was some transfer of fixed nitrogen from the broom to the *Pinus radiata*. However as total annual nitrogen uptake by the trees was restricted by water stress to only 2 kg ha^{-1} , the quantities transferred represent only a small proportion of the total nitrogen fixed by the broom ($< 2 \%$).

Environmental influences on rates of fixation

Nitrogen fixation and %Nd_{fa} increased with soil temperature over the first half of the growing season from lows in winter to a seasonal maximum in summer. A similar response has been observed in field grown broom (Wheeler *et al.*, 1987), and laboratory tests have indicated that nitrogenase activity in this species will increase to maximum rates at 25°C before declining (Wheeler *et al.*, 1979). It has been found that high temperatures stimulate biological nitrogen fixation through increasing plant metabolism (Lie, 1981), nodule formation (Roughly and Dart, 1970), rhizobium growth and rates of infection (Kumarasinghe and Nutman, 1979).

It is likely that the initial decline in %Nd_{fa} during late spring was due to flowering. The observed two peaked pattern is consistent with other studies on broom (Wheeler *et al.*, 1987), *Alnus glutinosa* (Pizelle, 1984) and *Trifolium repens* (Masterson and Murphy, 1976), where the decline from the first peak corresponds with the commencement of flowering.

The decline in %Nd_{fa} from a seasonal maximum during mid-summer was due to the development of seasonal water deficit (Fig. 3.2). This response is consistent with other studies on broom (Wheeler *et al.*, 1987), pasture species (Goh *et al.*, 1996) and

lupins (Sprent, 1973). Water stress has been found to reduce nitrogen fixation through depressing nitrogenase activity, nodule number and growth rate (Sprent, 1976).

Biomass increment of broom

Broom competed vigorously for water. Total annual evaporation in the treatment with broom was 25% higher than in the treatment without broom (Watt *et al.*, 2003). As a result of this high transpirational demand, root-zone water storage (W) in the treatment with broom fell from field capacity in mid-spring to minimum values by mid-summer. As rainfall was very sparse after this time W did not significantly increase from these minimum values until late autumn (Fig. 3.3).

Cessation of broom growth from mid-summer to late autumn was caused by complete depletion of the water table over this period. This was confirmed by measurements of stomatal conductance, taken at the start of the drought period. Water stress at this time induced almost complete stomatal closure in the leaves at midday, and average daily values were 87% lower than those recorded at the start of spring (0.035 vs $0.279 \text{ mol m}^{-2} \text{ s}^{-1}$). On sites in Canterbury where water is less limiting, broom shoot extension has been found to continue until the end of autumn (Williams, 1981).

The comparatively low values of broom growth reported highlight the importance of root-zone water content in regulating growth in this species. The annual biomass increment of $4\ 700 \text{ kg ha}^{-1}$ was three-fold lower than average yearly increments for natural broom communities growing on wetter sites in Oregon and Scotland (Wheeler *et al.*, 1987). Although these differences may be attributed partially to the greater age of these stands (2-4 yrs in Oregon, and 3-5 years in Scotland) this comparison does suggest that biomass growth on this study site was limited by seasonal water deficits. This is supported by measurements of broom height growth reported elsewhere in the literature. At age two years broom height has been found to range from 0.5 m on very drought prone riverbeds (Williams, 1981) to 3.0 m on sites in the Central North Island, New Zealand where water does not significantly limit plant growth (Kimberley and Richardson, 2003). The height of broom recorded in this study after two years (0.6 m) was at the lower end of this range.

Influence of broom on tree growth

Competition by broom for site resources completely outweighed any benefits to the tree resulting from nitrogen transfer. Annual biomass increment of trees in plots with broom was 14-fold lower than that of trees in broom-free plots. This loss in biomass has been previously found (see Chapter Two) to be correlated strongly to seasonal changes in predawn needle water potential ($r^2 = 0.91$) suggesting water stress induced by the presence of broom was the primary regulator of tree growth in this treatment. It is also possible that broom retarded tree growth through competition for nitrogen as the estimated soil uptake by the broom of $29 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ considerably exceeded rates of transfer ($2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). However this seems unlikely as foliar [N] of needle samples taken at the end of this study exceeded levels considered to be limiting to tree growth (Richardson *et al.*, 1996).

Long term influence of broom on tree growth

The potential of broom to enhance growth of *Pinus radiata* after the juvenile stage depends largely on root-zone water availability. In dryland areas broom is still able to reduce growth of *Pinus radiata* after it is overtopped, through competition for water (Richardson *et al.*, 2003). Although broom dies out after canopy closure nitrogen released to the soil in dry areas may not be fully utilised by conifers, as water stress almost always impairs nutrient uptake (Nambiar and Sands, 1993). In environments where water is relatively abundant, competition for light and nitrogen by broom will rapidly diminish when it is overtopped. As conifer growth after this time will largely be determined by nutrient supply, nitrogen released upon the death of the broom is likely to enhance tree growth, if these sites are deficient in nitrogen. Under these circumstances the benefits of controlling broom at establishment, beyond the point necessary to ensure adequate tree growth and survival, may be questionable.

CHAPTER FOUR

MODELLING THE INFLUENCE OF WEED COMPETITION ON THE GROWTH OF YOUNG *PINUS RADIATA* AT A DRYLAND SITE³

INTRODUCTION

Pinus radiata D. Don is the most widely planted forest species in New Zealand occupying approximately 1.7 million hectares throughout the country (N.Z.F.O.A. 2002). Research has shown that higher early growth rates are attained through adoption of management practices that allow trees greater access to site resources, such as nitrogen, water and light (Squire, 1977). Weed control plays a critical role in crop establishment and, as a management practice, is often the most influential on the rate of early crop growth (Mason and Whyte, 1997; Zhao, 1999).

The beneficial effect of weed control on *Pinus radiata* growth prior to canopy closure has been widely documented. Almost all of these studies report large volume gains which range from 25-fold one year after transplanting to 80% after ten years (Richardson, 1993). On sites where water is not limiting, Richardson *et al.* (1996) found that juvenile tree growth was most restricted by tall, fast growing competitors such as buddleia (*Buddleja davidii* Franchet) and broom (*Cytisus scoparius* L.). In contrast, herbaceous broadleaf weed species have the most detrimental influence on juvenile tree growth in dryland areas (Richardson *et al.*, 1993, 1997). Although the influence of weeds on tree growth declines with increasing age (Sands and Nambiar, 1984), there is some evidence to suggest that growth gains attained during the juvenile phase are maintained throughout the length of the rotation (Snowdon and Khanna, 1989; Balneaves and McCord, 1990; Mason and Milne, 1999).

Empirical models of juvenile *Pinus radiata* growth, sensitive to a range of site qualities and treatments, have been developed for both wet (Mason and Whyte, 1997;

³ This chapter is in press with *Forest Ecology and Management* as Watt, M., Whitehead, D., Richardson, B., Mason, E.G., and Leckie, A.C.

Mason, 2001) and dryland sites (Zhao, 1999). These models use regression techniques to derive growth equations which best fit the observed data. While these models contain no explicit representations of the interception of solar radiation, water use or carbon allocation, they are widely used by managers as they are easy to parameterise and provide reasonably accurate predictions of tree growth. However, such models are often limited in their general applicability and do little to elucidate the mechanisms by which weeds retard tree growth.

Development of more biologically realistic growth models requires specific knowledge of the mechanisms of interaction between trees and competitors, which will vary by site and weed species. Understanding these interactions is a two stage process which involves investigation into how weeds alter resource availability, and how the trees respond to this change in resource availability (Goldberg, 1996).

Using this approach, the influence of a range of common weed species on juvenile tree growth has been studied at a site with high rainfall in the Central North Island. It was found that weed species reduced juvenile tree growth primarily through restriction of solar radiation reaching the tree crowns (Richardson *et al.*, 1996). A competition index, negatively related to radiation availability, was derived from measurements of weed height relative to that of the trees, proximity of the weeds to the tree and weed abundance. Tree growth from time of planting to age three was then modelled as a function of this competition index and tree size (Kimberley and Richardson, 2001).

On dryland sites, water availability is the main constraint to tree development. Myers (1988) calculated a water stress integral, S_{ψ} , from cumulative measurements of predawn needle water potential, ψ_e . The water stress integral was then used to account for almost all of the variation in basal area increment of a stand subjected to a range of irrigation and fertilisation treatments.

Given the importance of water availability in regulating productivity on dryland sites, the water balance model may provide a useful process-based approach for modelling the influence of weeds on juvenile tree growth. Water balance models have been used to partition the components of evaporation and model root-zone water storage in both mature (Whitehead and Kelliher, 1991; Walcroft *et al.*, 1997) and juvenile (Yusuna *et al.*, 1995) stands of *Pinus radiata*. These models have also been included as components of highly parameterised process-based models to predict growth of mature

Pinus radiata on dryland sites (Walcroft *et al.*, 1997; Arneth *et al.*, 1999). However, there have been few attempts to use a water balance modelling approach to predict growth of *Pinus radiata*, during the juvenile phase, at which time trees are most sensitive to water stress (Sands and Nambiar, 1984).

An experiment on the Canterbury plains, New Zealand, was established to

- (i) quantify the effect of broom competition on growth of *Pinus radiata* at a dryland site
- (ii) use a water balance modelling approach, incorporating evaporation and transpiration, to determine which components are most influenced by the presence of broom and
- (iii) determine if root-zone water storage could explain growth differences of trees in plots with and without broom.

METHODS

Description of model

A daily water balance model was used to calculate root-zone water storage (W) on the i th day as

$$W_i = W_{i-1} + P_i - E_{ti} - E_{twi} - E_{bi} - E_{bwi} - E_{gi} - F_i \quad (4.1)$$

where P_i is rainfall, E_{ti} is transpiration from the tree canopy, E_{twi} evaporation from the wet tree canopy, E_{bi} transpiration from the broom canopy, E_{bwi} evaporation from the wet broom canopy, E_{gi} evaporation from the soil surface, and F_i drainage from the root zone (Whitehead *et al.*, 2001). Surface run off was assumed to be insignificant.

Transpiration from the tree canopy was calculated using the simple diffusion equation

$$E_t = D g_{st} L_t \quad (4.2)$$

where D is the air saturation deficit, g_{st} is the average stomatal conductance and L_t is leaf area index. The relationship between stomatal conductance and air saturation deficit was modelled using the function described by Lohammer *et al.* (1980) as

$$g_{st} = \alpha g_{stmax} (1 + (D - D_{smin})/D_{0t})^{-1} \quad (4.3)$$

where g_{stmax} describes maximum stomatal conductance, and D_{0t} is the sensitivity of g_{st} to D , when $D > D_{smin}$ (value of D below which g_s is constant). The same procedure was used to calculate stomatal conductance (g_{sb}) and then transpiration (E_b) for the broom canopy from the variables g_{sbmax} , L_b , D_{0b} .

The coefficient α was used to reduce stomatal conductance as root-zone water storage declined. Root-zone volumetric water content on the i th day, $\theta_i (=W_i/[r(1 - c)])$, was calculated from root zone depth, r , and fractional stone content of the soil, c . The value of the coefficient α was set to 1 at maximum values of θ (θ_{max}) and was not reduced until θ declined to a threshold value (θ_t). As θ progressively declined below this threshold, α was reduced linearly from 1 to reach 0 at the minimum value of θ (θ_{min}).

The aerodynamic roughness of broom and *Pinus radiata* foliage is likely to result in good mixing within the canopy microclimate. For this reason, it was assumed above-canopy values of D would be applicable to both species. The validity of this assumption was confirmed by measurements which showed no significant differences in D above and within the broom and *Pinus radiata* canopy.

Evaporation from the soil, E_g , was calculated from the available energy beneath the tree and broom canopies, G_g , as,

$$E_g = \min[\alpha, \beta] (\tau s G_g / [\lambda(s + \gamma)]) \quad (4.4)$$

where the term $s G_g / [\lambda(s + \gamma)]$ is the equilibrium rate of evaporation. The coefficient τ describes the degree of coupling of the soil surface with the air above the canopy (Kelliher *et al.*, 1990), s is the slope of the relationship between saturated vapour pressure and temperature at a given air temperature, λ is the latent heat of vaporisation, and γ is the psychrometric constant. Using Beers Law, G_g was calculated from $(1 - e^{-k(Lt+Lb)})G_a$ where G_a is the available energy above the canopy (assumed to be 70% of shortwave radiation) and k is the light extinction coefficient (assumed to be 0.5 for a spherical leaf angle distribution). The coefficient α was used to reduce E_g with declining W , using the same procedure as previously outlined for stomatal conductance in Equation 4.3. The decline in E_g with drying of the soil surface (Jackson and Wallace, 1999) was modelled through the

use of the coefficient β which describes the reduction in E_g in response to the number of days after rain. In Equation 4.4, the term $\min[\alpha, \beta]$ refers to the minimum of these two coefficients. Soil surface evaporation and transpiration were reduced to 75% of their potential rates on days when rain occurred. Transpiration was also reduced by 50% on days when an air temperature $< 0^\circ\text{C}$ was recorded.

Evaporation from the wet broom canopy was modelled as a function of L_b and P , using the following function

$$E_{bw} = p_1(P)^{p_2}(L_b)^{p_3} \quad (4.5)$$

where the parameters p_1 , p_2 , and p_3 are determined empirically.

Drainage from the root zone was assumed to be zero when $\theta_i \leq \theta_{\max}$ and equal to rainfall reaching the soil when $\theta_i > \theta_{\max}$.

Daily weather data required for the water balance model includes total rainfall, solar radiation, minimum and mean air temperature and average air saturation deficit. The model also requires values for the twelve parameters $g_{st\max}$, D_{0t} , $g_{sb\max}$, D_{0b} , θ_t , r , c , θ_{\max} , θ_{\min} , p_1 , p_2 , and p_3 (Table 4.1) and seasonal measurements of L_t and L_b .

Table 4.1. Values used for parameters in the water balance model. See text for explanation of the symbols.

Parameter	Value	Units
$g_{st\max}$	0.25	$\text{mol m}^{-2} \text{s}^{-1}$
D_{0t}	0.94	kPa
$g_{sb\max}$	0.46	$\text{mol m}^{-2} \text{s}^{-1}$
D_{0b}	0.32	kPa
$\theta_t (E_g, E_t, E_b)$	0.25, 0.23, 0.16	$\text{m}^3 \text{m}^{-3}$
r	300	mm
c	0.2	$\text{m}^3 \text{m}^{-3}$
θ_{\max} (with broom, without broom)	0.33, 0.41	$\text{m}^3 \text{m}^{-3}$
θ_{\min} (with broom, without broom)	0.08, 0.08	$\text{m}^3 \text{m}^{-3}$

Site description and treatments

The model was used to estimate daily water balance from June 2000 to June 2001, at an experimental site located near Hororata on the Canterbury plains, 60 km west of Christchurch, New Zealand (latitude 43°34' S, longitude 171°55' E, elevation 210 m asl).

The soil at the site, which is classified as a Lismore stony silt loam, (Kear *et al.*, 1967) is free draining and of low fertility. Water storage within the stony soil ($c = 0.2$) was limited to approximately 70 mm in the main root zone (0.3 m soil depth). At depths lower than 0.3 m, volumetric stone content increased to over 50%, and root density was very low ($< 3\%$ of total mass). Seasonal water deficits are characteristic for this widely distributed soil and very common on the Canterbury plains, where the regular occurrence of hot dry northwest winds during spring and summer causes high potential evaporative demand. Long term average rainfall at the site is relatively low (797 mm yr^{-1}) and evenly distributed throughout the year ($66.4 \pm 2.2 \text{ mm month}^{-1}$, New Zealand Met. Service, 1983).

The experiment was located within a ~ 20 ha *Pinus radiata* plantation, established on the flat site during winter of 1999. Residue (stumps, branches) from the previous crop of *Pinus radiata* had been cleared into E-W orientated windrows, spaced approximately 50 m apart. Trees were planted between the windrows along ripped lines in E-W facing rows at a spacing of 4 x 2 m.

During summer 1999, 12 plots were established on the west side of the plantation, where natural regeneration of the woody weed broom was good. The 12 plots were divided into 6 blocks, and two treatments were assigned randomly to each block. Treatments included no control of the weeds and complete removal of all weeds within the plot. Each main plot, which included 24 trees, was completely surrounded by a buffer of seedlings subjected to the same treatment.

Weed control was achieved by applying 6.25 kg of terbuthylazine mixed with 900 g of clopyralid and 300 g of haloxyfop in 250 l ha^{-1} of water. This herbicide was applied to designated plots to eliminate existing vegetation, which consisted mainly of broom, interspersed with some herbaceous broadleaved weeds. After spraying, any weed regrowth was removed by a combination of hand weeding and spot herbicide application.

Meteorological sensors were installed on a 3 m tower, located in a small clearing, adjacent to the experimental plots. Hourly measurements of photosynthetically active

photon flux density, air temperature and relative humidity were made above the canopy. In treatment plots adjacent to the tower a tipping bucket raingauge on a 1.5 m stand measured above-canopy rainfall. Root-zone water storage in both treatments was recorded by two (1 per treatment) time domain reflectometry sensors (Aquaflex, model SI. 60, Streat Instruments, Lincoln, New Zealand) installed within the tree rows, at a depth of 0.2 m. The maximum and minimum measured root-zone water storage in each treatment were used to define θ_{\max} and θ_{\min} .

Leaf area index of Pinus radiata and broom

A prediction equation for *Pinus radiata* foliage area was developed from destructive sampling, undertaken during the winter periods of 2000 and 2001. During each period, a total of 20 trees were selected ($n = 10$ per treatment) covering the size range existing in each treatment. The diameter of each tree was measured before it was extracted and divided into its component parts. All foliage samples were oven dried at 70°C until constant mass was reached, then weighed. Following Beets (1977), specific leaf area was determined on a foliage subsample from measurements of volume, dry weight and average fascicle length. Values for foliage area are presented on the basis of half the total surface area. From these measurements the relationship between groundline basal area, A_b , ($\text{m}^2 \text{ tree}^{-1}$) and foliage area, A_f , ($\text{m}^2 \text{ tree}^{-1}$) was determined as $A_f = -0.0367 + 2.317A_b$, $P < 0.0001$, $r^2 = 0.99$.

Development of foliage area over the growing season was scaled using phenological measurements of needle length. Estimates of seasonal needle growth were made on ten trees per treatment, starting in spring (September). One branch was chosen randomly on each tree, and a datum point was marked at the base of the leading bud. At two weekly intervals, the length of randomly selected fascicles were measured over the entire length of the current shoot.

The seasonal increase in mean needle length, l , was modelled as a function of the number of days after elongation started, t . This was undertaken using the von Bertalanffy equation (Richards, 1959), which was fitted to the data by a non-linear least squares procedure using

$$l = l_m (1 - e^{-a_1 t})^{a_2} \quad (4.6)$$

where l_m is the maximum needle length, and a_1 and a_2 are parameters. Differentiation of the von Bertalanffy equation allows the calculation of maximum rate of needle growth at the point of inflexion in the relationship, l_i , and the value of t when this occurs, t_i . The time taken to reach 95% of the maximum needle length, t_{95} , was also calculated through rearrangement of Equation 4.6. Needle growth of individual trees was modelled using Equation 4.6 and analysis of variance was then used to investigate treatment effects on the parameters l_m , l_i , t_i and t_{95} .

At monthly intervals, leaf area index of the broom, L_b , was measured directly using a canopy analyser (LAI-2000, Li-Cor Inc., Lincoln, NE, USA). It was assumed that foliage area within the canopy was distributed randomly. The plots were stratified into between and within row components as the influence of a strip herbicide applied after planting was still apparent. L_b was measured at 24 locations selected randomly within each component, and these plot level estimates were modelled against time using a segmented regression procedure (Hunt, 1982). Seasonal estimates of L_b for the entire plot were obtained by averaging modelled values for both components.

Wet canopy evaporation

Net rainfall reaching the soil surface was measured for both broom and *Pinus radiata* components using six plastic troughs ($n = 3$ per treatment) laid out randomly in a pair of treatment plots. Data were collected from 33 rainfall events, when it was certain that the canopy and stems were dry before and after the event.

Stomatal conductance

Stomatal conductance for broom and *Pinus radiata* was measured by placing foliage in a clear top curvette attached to a gas exchange system (model LI 6400, Li-Cor Inc., Lincoln, NE, USA). Measurements were taken from the youngest fully expanded foliage over the course of a day on 14 separate occasions from spring (September) to early winter (April). Throughout the day, measurements of stomatal conductance for *Pinus radiata*, g_{st} , were repeatedly made on 20 shoots distributed throughout the canopy of 10 trees. Single measurements of stomatal conductance for broom, g_{sb} , were made on 50 leaves within the upper broom canopy. Measurements of *Pinus radiata* fascicle area were made following the procedures described by Beets (1977). Leaf area of broom was

measured using an area meter (model LI 3100, Li-Cor Inc., Lincoln, NE, USA). Values of conductance for both species are expressed on the basis of half the total surface area.

Evaporation from the soil surface

Evaporation from the soil surface (E_g) was calculated from measurements of weight loss in three plastic walled lysimeters (150 mm diameter and 120 mm deep) placed in the soil in a plot without broom. Measurements of E_g were made for periods of up to three days following rainfall events. Gravimetric samples taken after each set of measurements indicated no significant differences in W for soil within and surrounding the lysimeters.

Analysis of tree growth

Stem diameter at ground level was measured for all trees at monthly intervals over the year long measurement period. Analyses used data collected over spring and summer, which was divided into three periods each covering a duration of two months. Basal area growth was calculated as the difference in basal area between the start and the end of the period. Daily root-zone water deficit was calculated as $W_{\max} - W_i$. These values were summed for each of the two month periods to give an integrated root-zone water deficit, $S_w = \Sigma(W_{\max} - W_i)$, using the approach of Myers (1988).

In a study of this nature, where time series measurements are taken from the same sample plots, the strong effect of initial basal area needs to be removed before subsidiary influences on basal area growth can be examined. To remove this effect, a linear regression of basal area growth, ΔA_b , ($\text{m}^2 \text{ tree}^{-1}$) against initial basal area, A_b , ($\text{m}^2 \text{ tree}^{-1}$) was determined for the treatment without broom, as $\Delta A_b = -3.9\text{E-}05 + 0.81A_b$, $P < 0.0001$, $r^2 = 0.98$. Fractional basal area growth for the trees growing with broom was then calculated as the ratio between actual basal area growth and that predicted by the regression line, given initial basal area.

As the analysis used data obtained from repeated measurements on individual sample plots, hypothesis testing using a fixed effects model was inappropriate. The temporal autocorrelation in datasets of this type leads to underestimation of regression coefficient standard errors, invalidating normal statistical hypothesis tests (West *et al.* 1984). To solve this problem, hypothesis testing was undertaken using a procedure

(PROC MIXED) which accounts for autocorrelation by modelling variances and covariance of the data through the use of covariance parameters (SAS Institute Inc., 1996).

RESULTS

Tree basal area growth

Treatment differences in basal area, which became significant ($P = 0.0347$) from mid-winter (July) onwards, diverged markedly after mid-spring (Fig. 4.1). In plots without broom, tree basal area increased 12-fold over the course of the year, reaching maximum growth rates during late summer (February). In contrast, basal area of trees growing with broom increased only two-fold during the year. After reaching the highest rates in early spring (September), growth in this treatment gradually declined and virtually ceased during the very dry summer and autumn period (Fig. 4.1).

Climate over the growing season

During the measurement year, mean daily temperature was 13.9°C, with the daily maximum of 28.2°C occurring in late summer (February) and daily minimum of 1.4°C during mid-winter (July). Frosts were recorded on 83 days and most frequently occurred over the late autumn and winter period. Air saturation deficit followed a similar seasonal pattern to temperature, with the maximum daily value (2.5 kPa) occurring during late summer (February). Incident irradiance totaled 2.4 GJ m⁻² for the year and reached a maximum daily value in mid-summer of 15.7 MJ m⁻².

The annual precipitation of 648 mm was lower than average and unevenly distributed throughout the year. The very wet conditions which occurred during late winter continued over spring, with rainfall during this period exceeding long term averages. In contrast, early to mid-summer was relatively dry, and rainfall was even less frequent from late summer to late autumn. During this latter three month period, which was the driest since records began in 1890 (New Zealand Met. Service database), only 38 mm of rain was recorded at the site.

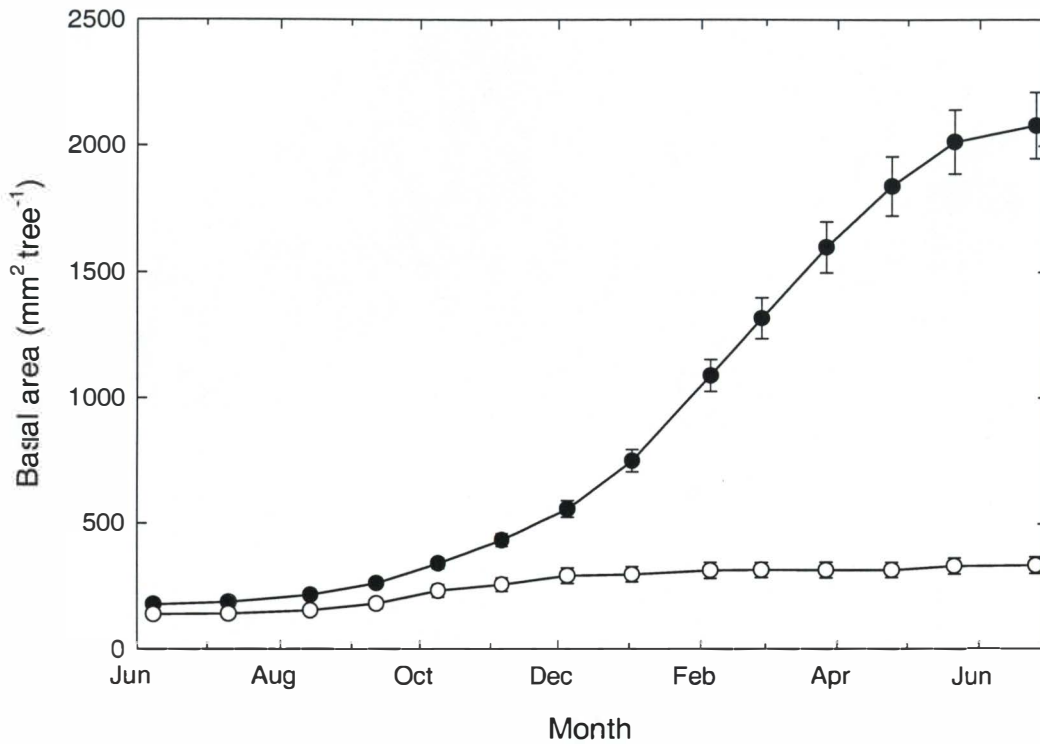


Figure 4.1. Changes in basal area of trees growing without broom (filled symbols) and with broom (open symbols) over the course of the growing season. Each point shown is the mean \pm standard error of six sample plots.

Seasonal development of Pinus radiata and broom foliage area

Leaf area index of the *Pinus radiata* increased from 0.05 to 0.58 m² m⁻² in the treatment without broom, over the course of the growing season. Annual changes in leaf area index for trees growing with broom were much lower increasing from 0.04 to 0.09 m² m⁻². Although the rate differed, the timing of needle elongation during the spring flush was similar for trees in both treatments (Fig. 4.2). The analysis of variance on parameters derived from the von Bertalanffy equations revealed two significant treatment differences. Trees growing without broom developed longer needles ($l_m = 96$ mm vs 39 mm) at a faster maximum rate ($l_i = 0.88$ mm day⁻¹ vs 0.33 mm day⁻¹) than trees growing with broom. No significant treatment differences were noted between the time taken to reach the fastest growth rate, t_i , or 95% of the maximum needle length, t_{95} . For

trees growing without broom there was a small autumn flush, but this did not occur for trees in plots with broom (Fig. 4.2)

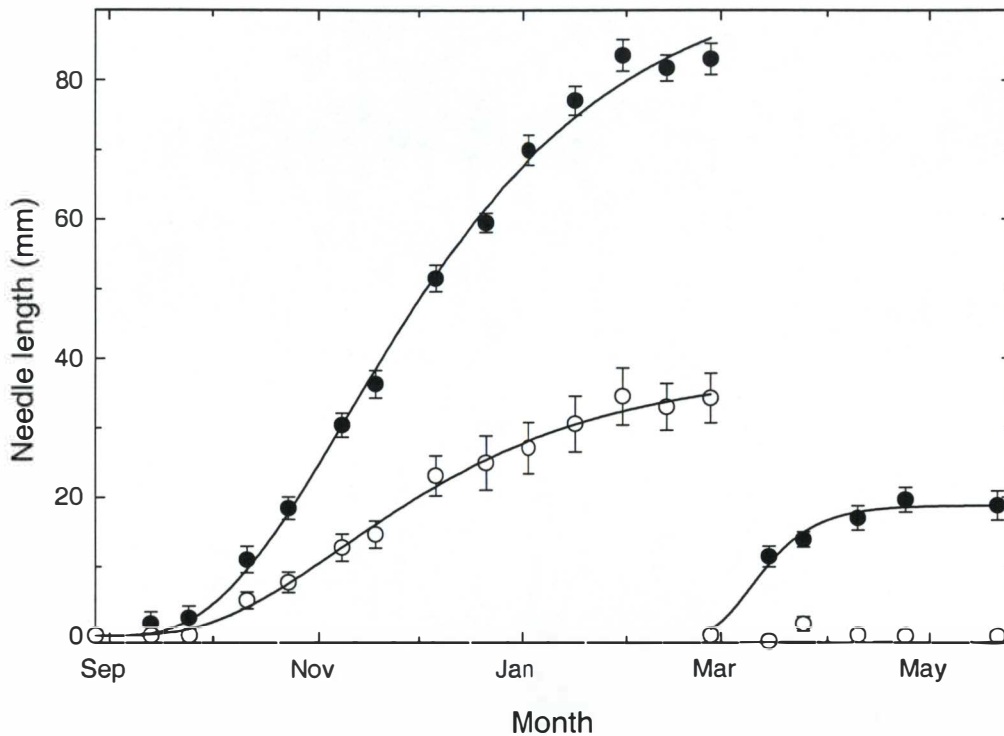


Figure 4.2. Seasonal increase in mean needle length (l) for trees growing without broom (filled symbols) and with broom (open symbols). Each point shows mean needle length \pm standard error from measurements on 10 trees, for growth flushes starting in spring and autumn. The lines were fitted using Equation 4.6. For the trees growing without broom the parameters l_m (mm), a_1 and a_2 are 95.8, 0.02, 4.40 (spring flush) 20.5, 0.038, 0.81 (autumn flush) and for trees growing with broom values are 39.6, 0.019, 4.01 (spring flush).

Over the course of the growing season, leaf area index of the broom, L_b , increased five-fold. From starting values of $0.3 \text{ m}^2 \text{ m}^{-2}$, L_b increased exponentially over spring and early summer, reaching a seasonal maximum of $1.5 \text{ m}^2 \text{ m}^{-2}$ in mid-summer. Leaf area index of the broom steadily declined from late summer to a value of $1.2 \text{ m}^2 \text{ m}^{-2}$ during late autumn as a result of leaf loss over this very dry period.

Wet canopy evaporation

Evaporation from the wet broom canopy, E_{bw} , was positively and significantly ($P < 0.0001$) related to both L_b and P . Equation 4.5 fitted well to the measured data with little apparent bias (Fig. 4.3), using parameter values for p_1 , p_2 , and p_3 of 0.34, 0.96, and 0.59 respectively. As net rainfall was found to be equal to above-canopy rainfall in plots without broom, it was assumed that evaporation from the wet tree canopy was equal to 0.

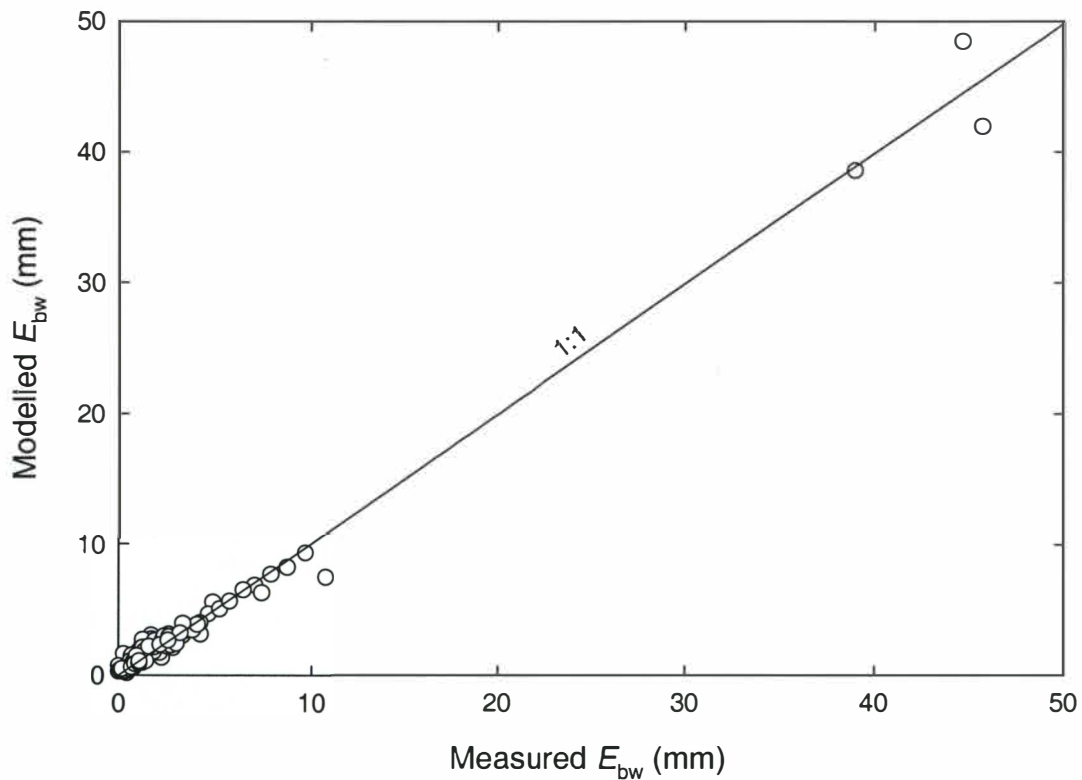


Figure 4.3. Relationship between measured and modelled evaporation from the wet broom canopy (E_{bw}). The line shows the 1 : 1 relationship.

Stomatal conductance

In both species, stomatal conductance decreased with increasing D (Fig. 4.4). For almost all relationships, the decrease in stomatal conductance did not occur until D reached values of ~ 0.5 kPa. The two exceptions occurred during very dry conditions ($\theta = 0.11 \text{ m}^3 \text{ m}^{-3}$), when an immediate decline in g_s with increasing D was noted (Fig. 4.4) in both broom ($D_{smin} = 0.23$ kPa) and *Pinus radiata* ($D_{smin} = 0.05$ kPa).

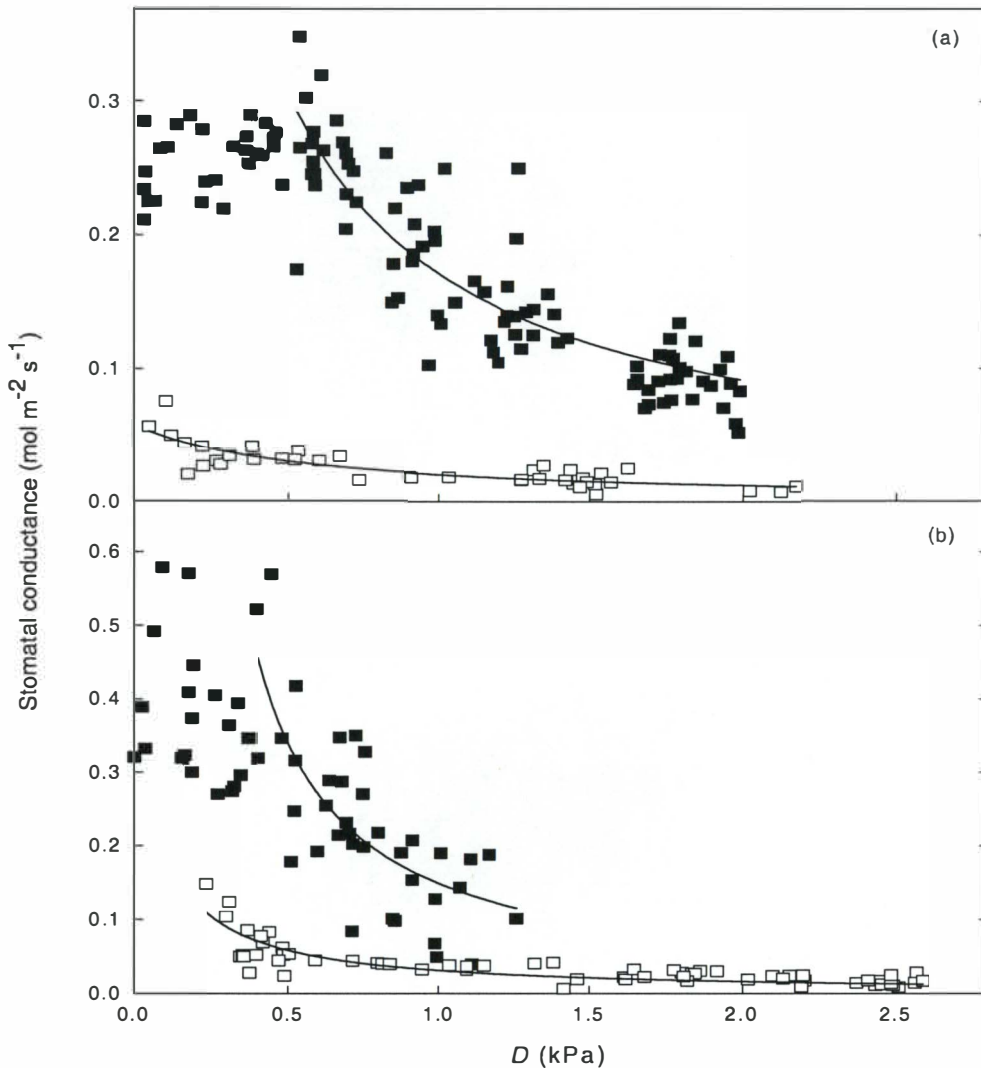


Figure 4.4. The relationship between stomatal conductance and air saturation deficit (D) for foliage of (a) *Pinus radiata* and (b) broom. For (a) filled symbols represent root zone water content (θ) of $0.26 \text{ m}^3 \text{ m}^{-3}$ and open symbols represent $\theta = 0.11 \text{ m}^3 \text{ m}^{-3}$. For (b) filled symbols represent $\theta = 0.16 \text{ m}^3 \text{ m}^{-3}$ and open symbols represent $\theta = 0.11 \text{ m}^3 \text{ m}^{-3}$. The lines were fitted to the data using Equation 4.3, and the parameters $g_{s\max}$, ($\text{mol m}^{-2} \text{s}^{-1}$) D_0 and $D_{s\min}$ (kPa) are (a) 0.31, 0.64, 0.50 ($\theta = 0.26 \text{ m}^3 \text{ m}^{-3}$) and 0.053, 0.58, 0.05 ($\theta = 0.11 \text{ m}^3 \text{ m}^{-3}$) and (b) 0.46, 0.29, 0.40 ($\theta = 0.16 \text{ m}^3 \text{ m}^{-3}$) and 0.11, 0.36, 0.23 ($\theta = 0.11 \text{ m}^3 \text{ m}^{-3}$). For purposes of revealing this relationship only measurements taken when incident radiation was $> 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ are included.

Although variation in D_0 was noted between species and over the range in θ , differences were not significant. The sensitivity of stomatal conductance to D was lower

in *Pinus radiata* than that for broom as D increased, with values of D_{0t} and D_{0b} of 0.94 kPa and 0.32 kPa, respectively. Sensitivity to D declined in both species as root-zone water storage decreased; this trend was most marked in *Pinus radiata* with D_{0t} ranging from 0.63 kPa ($\theta = 0.26 \text{ m}^3 \text{ m}^{-3}$) to 1.15 kPa ($\theta = 0.16 \text{ m}^3 \text{ m}^{-3}$).

Over comparable values of θ , maximum stomatal conductance was significantly higher for broom than that for *Pinus radiata*. These differences were most pronounced during moderately dry conditions ($\theta = 0.16 \text{ m}^3 \text{ m}^{-3}$) with values for g_{sbmax} ($0.46 \text{ mol m}^{-2} \text{ s}^{-1}$) exceeding those for g_{stmax} ($0.13 \text{ mol m}^{-2} \text{ s}^{-1}$) by threefold.

In both species, maximum stomatal conductance significantly declined with decreasing θ . For *Pinus radiata*, g_{stmax} was relatively insensitive to soil water depletion until θ reached a threshold value of $0.23 \text{ m}^3 \text{ m}^{-3}$ (θ_t). As θ was reduced below this threshold, there was a strong ($r^2 = 0.99$) significant ($P < 0.0001$) linear decline in g_{stmax} to minimum measured values (Fig. 4.5). In broom, maximum stomatal conductance, g_{sbmax} , responded similarly to decreasing θ .

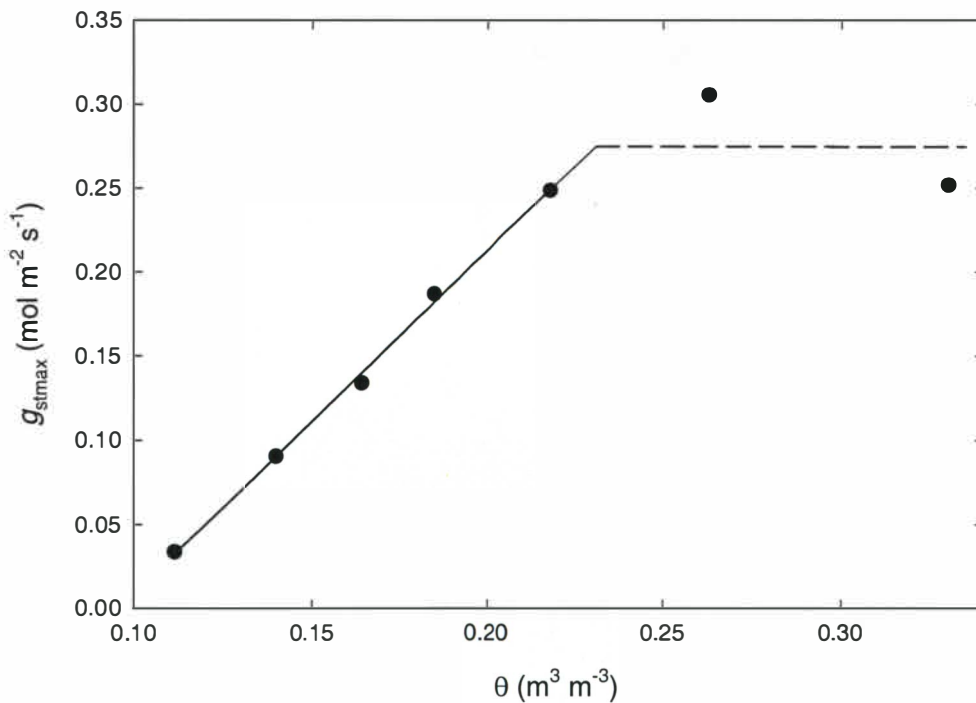


Figure 4.5. The relationship between maximum stomatal conductance of *Pinus radiata* (g_{stmax}) and root-zone volumetric water content (θ). The solid fitted line below the threshold ($\theta_t = 0.23 \text{ m}^3 \text{ m}^{-3}$) is a linear equation with slope of two. Above θ_t it is assumed that g_{stmax} is equal to $0.28 \text{ mol m}^{-2} \text{ s}^{-1}$ (dashed line).

Evaporation from the soil surface

Under well-watered conditions, measured E_g declined over the course of a drying cycle after rainfall had ceased. On the first day after rainfall, the ratio of E_g to the equilibrium rate, τ , was 1.46, when $\beta = 1$. During the next two days, β decreased to values of 0.49 and 0.29 respectively.

Treatment effects on water balance

Total annual evaporation was 92 mm higher in the treatment with broom, with monthly losses significantly exceeding those of the treatment without broom over winter and spring (Table 4.2). The monthly rate of total evaporation in the treatment with broom peaked at 82 mm during late spring and fell to a minimum of 11 mm in early autumn. In the treatment without broom, monthly total evaporation increased from a minimum of 9 mm in mid-winter to a maximum of 73 mm in early summer (Table 4.2).

Table 4.2. Monthly modelled estimates of the components of evaporation (mm month^{-1}) in treatments with and without broom over the course of the year. The symbols P , E_g , E_t , E_b , and E_{bw} respectively refer to rates of rainfall, evaporation from the soil surface, transpiration from the tree canopy, transpiration from the broom canopy, and evaporation from the wet broom canopy. Data shown represent treatment averages of six plots.

Month	P	Without broom			With broom			
		E_g	E_t	Total	E_g	$E_t + E_b$	E_{bw}	Total
Jun	42	9	1	10	8	6	4	18
Jul	24	9	0	9	8	4	4	16
Aug	213	16	0	16	14	4	31	49
Sep	69	27	1	28	23	9	13	45
Oct	32	42	3	45	34	19	7	60
Nov	85	50	7	57	33	26	23	82
Dec	40	57	16	73	21	25	14	60
Jan	52	42	17	59	12	25	21	58
Feb	14	26	11	37	4	9	6	19
Mar	9	12	4	16	2	5	4	11
Apr	15	7	3	10	2	4	6	12
May	53	10	5	15	5	13	19	37
Total	648	307	68	375	166	149	152	467
% P		47	10	58	26	23	23	72

The higher total annual evaporation in the treatment with broom was due both to increased rates of total transpiration and evaporation from the wet broom canopy, E_{bw} . In this treatment, total transpiration increased concurrently with L_b to a daily maximum of 2.0 mm in mid-summer, before significantly declining in response to low W (Fig 4.6). Annual transpiration in the treatment without broom was 54% lower, reaching peak values of 0.8 mm day⁻¹ in mid-summer (Fig. 4.6).

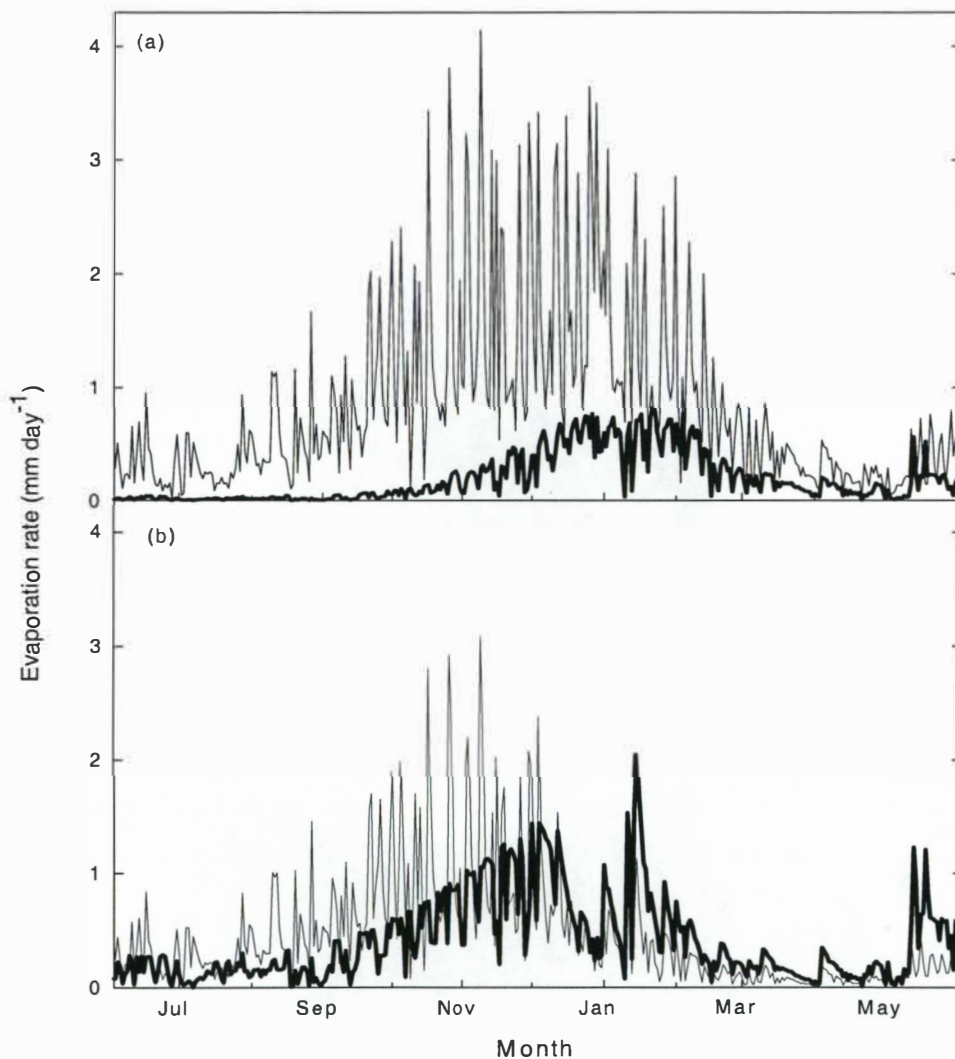


Figure 4.6. Modelled daily rates of total transpiration (thick line) and evaporation from the soil surface (thin line) in treatments (a) without and (b) with broom over the course of the year. Data shown represent treatment averages of six plots.

Annual values for E_{bw} were of a similar magnitude to total transpiration in the treatment with broom, comprising 33% of total annual evaporation. Over the course of the year, E_{bw} progressively increased with development of L_b , from 10% of above canopy rainfall in early winter to 44% during early autumn (Table 4.2).

Soil surface evaporation, E_g , was the largest component of water loss in the treatment without broom, accounting for 82% of total annual evaporation (Table 4.2). Rates of E_g within this treatment reached a maximum of 4.1 mm day^{-1} in late spring (Fig. 4.6). Although annual E_g was 46% lower in the treatment with broom, losses from this component still comprised the largest proportion of total annual evaporation (36%). Soil surface evaporation increased in this treatment to a daily maximum of 3.1 mm in late spring (Fig. 4.6). After this, E_g rapidly declined as development of L_b reduced the available energy reaching the soil surface. Soil surface evaporation was further constrained from late summer to mid-autumn by low W (Fig. 4.6).

Validation of the water balance model

In the plot with broom, W declined rapidly from mid-spring onwards, nearly reaching minimum values ($W_{\min} = 19.2 \text{ mm}$) by early-summer (Fig. 4.7). Apart from a transient increase over mid-summer, W did not significantly depart from W_{\min} until the end of autumn, when rain partially refilled the water table. Root-zone water storage in the plot without broom remained fairly high ($> 58 \text{ mm}$) until late summer. After this time, W gradually declined reaching a minimum of 24 mm at the end of autumn, before partially recharging after rain. In both treatments, modelled W corresponded closely to measured values over the course of the year (Fig. 4.7).

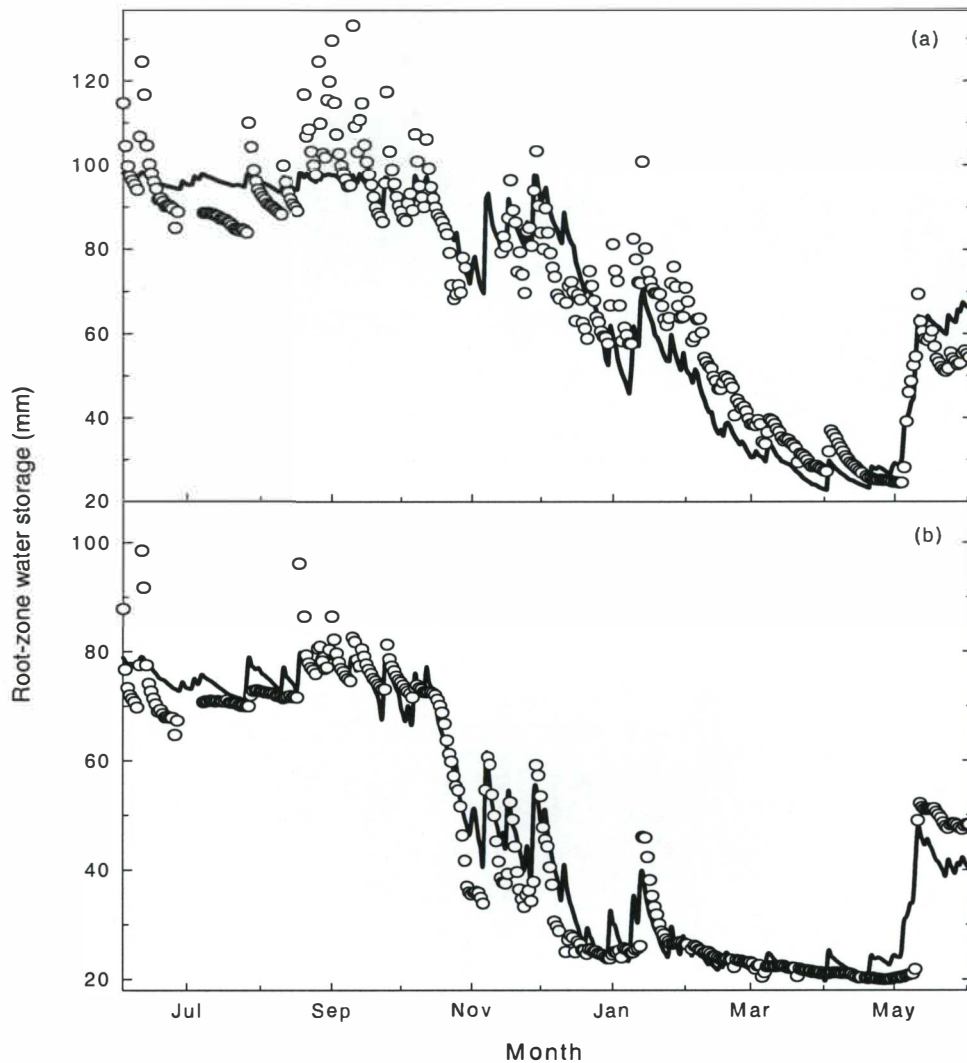


Figure 4.7. Comparison of modelled (continuous line) with measured (open symbols) daily root-zone water storage (W) for plots (a) without and (b) with broom over the course of the year.

Relationship between water availability and growth

Fractional basal area growth was significantly ($P < 0.0001$) correlated to integrated root zone water deficit, S_w (Fig. 4.8). Basal area growth was unconstrained until S_w reached 600 mm. Above this value, fractional basal area growth declined rapidly to 0.6 at S_w of 770 mm, after which reductions were slower until minimum values of ~ 0.1 at S_w of 3 100mm were reached. Extrapolation of the fitted line indicated basal area growth ceased when S_w reached 3 460 mm (Fig. 4.8)

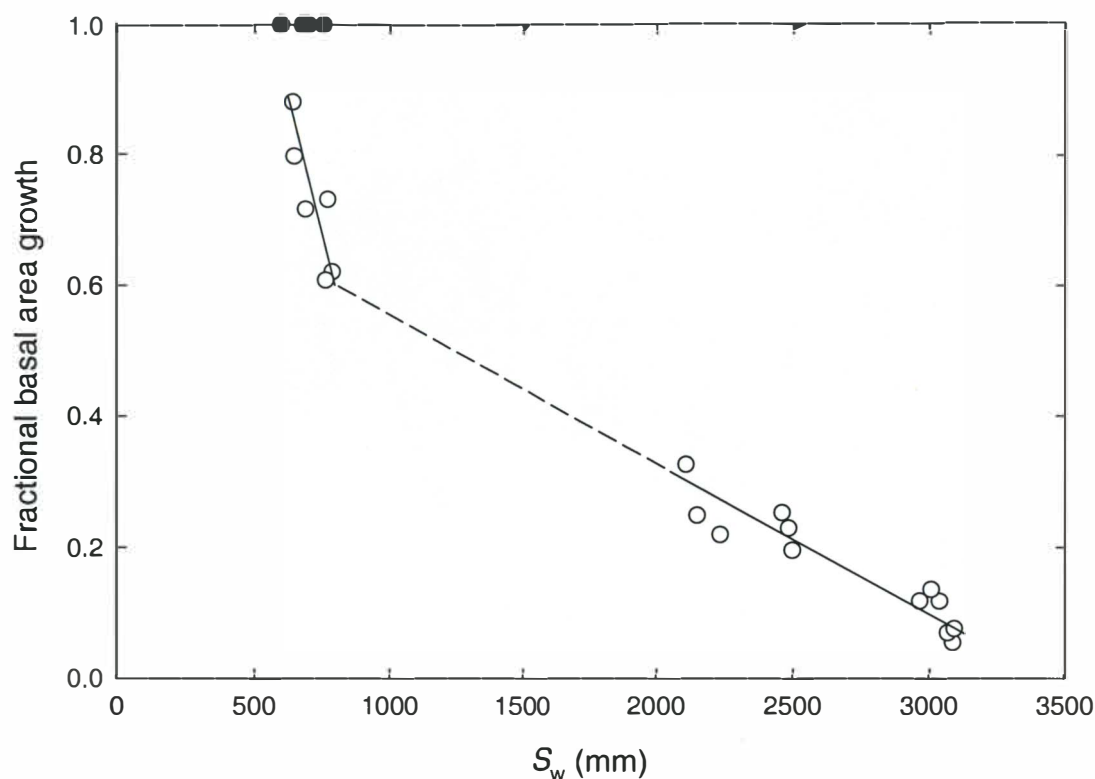


Figure 4.8. Relationship between integrated root-zone water deficit (S_w) and fractional basal area growth of *Pinus radiata*. For the treatment with broom (open symbols), data are for six plots, with measurements integrated over two monthly periods, three times during the growing season. Fractional basal area growth and two monthly S_w were averaged over all three periods for the six plots without broom (filled symbols).

DISCUSSION

The presence of broom reduced tree annual basal area increment by almost ten-fold. Although it is well known that broom adversely affects tree growth (Richardson *et al.*, 1993, 1996, 1997), reductions of this magnitude have not been reported previously. It is likely these comparatively low growth rates were due to the unusually dry conditions over summer and autumn of the measurement year, during which time only 183 mm of rain fell.

Growth of trees in the treatment without broom was largely unlimited by water stress. This was confirmed from measurements of predawn needle water potential taken

at two weekly intervals over the course of the year. Values did not fall below -0.96 MPa until late autumn, and were very similar to those reported for irrigated *Pinus radiata* (Myers, 1988). Other studies at dryland sites have also reported little effect of water deficit for juvenile trees growing in weed free plots (Sands and Nambiar, 1984; Richardson *et al.*, 1997).

The strong relationship between fractional basal area growth and S_w (Fig. 4.8) suggests losses in growth are almost entirely attributable to development of a more pronounced seasonal water deficit in the treatment with broom. The non-linear response of fractional basal area growth to S_w was of a similar form to the relationship found between water stress integral and basal area increment by Myers (1988).

Several other studies on dryland sites (Richardson *et al.*, 1993, 1997) have also suggested that growth reductions induced by broom are primarily mediated through competition for water. However the relative importance of competition for light on tree growth may increase after the second year as broom leaf area index increases and trees reduce water stress through accessing alternative sources of water deeper in the profile.

In the model it was assumed that parameters and relationships derived from measurements on individual plots are generally applicable for estimating water balance in all plots. As measurements of maximum root-zone water content, soil depth and stone fraction were very similar between replicates, it is unlikely that plot specific variation would have led to large errors in modelled root-zone water content.

The high annual estimates of E_{bw} indicate this is an important component of water balance for juvenile stands with tall, fast-growing competitors. Annual values of E_{bw} (23% of P) were more than twofold greater than those reported for ryegrass or lucerne understories growing beneath juvenile *Pinus radiata* (Yusuna *et al.*, 1995). As E_{bw} increased concurrently with L_b , losses from this source over the subsequent growing season are likely to exceed the maximum rates noted in this study (44% of P).

Soil surface evaporation, E_g , was the largest component of water loss for the treatment without broom. The ratio of E_g to the equilibrium rate on the day immediately after rainfall ($\tau = 1.46$) was very similar to values found by Kelliher *et al.* (1990), and the decline in E_g in the days following rainfall was consistent with other studies (Lascano and van Bavel, 1986; Jackson and Wallace, 1999). As E_g represents such a large

proportion of total evaporation in open young stands, incorporation of this modifier is essential for accurate modelling of W . In the treatment with broom, the significantly lower rates of E_g partially offset enhanced rates of E_{bw} and total transpiration.

Transpiration from the broom canopy, E_b , was a significant component of annual water balance in the treatment with broom. However, losses from this source were considerably lower than values reported for ryegrass and lucerne understories, where transpiration was found to be the largest component of water balance (Yusuna *et al.*, 1995). Transpiration from the broom canopy will increase with development of L_b over the subsequent growing season. However, increases in E_{bw} are likely to further reduce W which will result in a decrease in the ratio of E_b to E_{bw} .

The presence of broom reduced E_t by elevenfold. As D was assumed to be the same between treatments, 54% of the reduction in E_t was attributable to lower L_t while 46% was attributable to reductions in g_{st} . During periods of high W , g_{stmax} was at the upper end of the range reported by other studies. Similar values have been documented for well watered *Pinus radiata*, ranging in age from 1 to 14 years (Attiwill *et al.*, 1982; Thompson and Wheeler, 1992; Whitehead *et al.*, 1994), although somewhat lower values are also common in the literature (Benecke, 1980; Whitehead *et al.*, 1991). A significant linear decline in g_{stmax} was observed once a threshold root-zone water deficit had been reached (Fig. 4.5). Calculations of water storage indicated that 55% of the extractable soil water had been removed from the top 300 mm before g_{stmax} became limited. Similar threshold values have been reported in stands of 8 year old *Pinus radiata* (Arneth *et al.*, 1999), 41 year old *Pinus sylvestris* L. (Irvine *et al.*, 1998) and for a range of mature coniferous species (Kelliher *et al.*, 1998). The sensitivity of g_{st} to increasing D is consistent with results from other studies (Thompson and Wheeler, 1992; Whitehead, *et al.*, 1996; Miller *et al.*, 1998).

In conclusion, seasonal changes in root-zone water storage estimated from the water balance model agreed closely with measurements of W in both treatments. The strong link between W and basal area growth indicates that this approach will be useful for predicting the influence of weed competition on the growth of juvenile trees at sites where seasonal water deficits are pronounced.

CHAPTER FIVE

DEVELOPMENT OF A GENERALLY APPLICABLE JUVENILE TREE GROWTH MODEL SENSITIVE TO COMPETITION FROM WEEDS

INTRODUCTION

Pinus radiata D. Don is the most widely planted forest species within New Zealand. Plantations of this species, which occupy 1.7 million hectares throughout the country (N.Z.F.O.A., 2002), are located over a wide range of climatic and edaphic conditions. At one extreme the forests in the Central North Island receive high rainfall (1480 mm yr⁻¹; New Zealand Meteorological Service, 1983), and overlay very deep and fertile soils, with a high water storage (Beets *et al.*, 1991). In contrast a significant area of the plantation estate is found on dryland sites on the South Island east coast, where annual rainfall can be as low as 626 mm yr⁻¹ (New Zealand Meteorological Service, 1983) and soils are often very shallow, infertile and stony (Kear *et al.*, 1967).

Although the rate of stand development is strongly dependant on climate and edaphic conditions, growth rate within these forests can be manipulated to some extent through adoption of management practices that allow trees greater access to site resources. Research has shown that the greatest potential for improving growth rates in these forests is during the early stages of establishment prior to canopy closure. During this juvenile period, weed control plays a critical role and is often the most influential management practice on the rate of early crop growth (Mason and Whyte, 1997; Zhao, 1999).

The beneficial effect of weed control on *Pinus radiata* growth prior to canopy closure has been widely documented. Almost all studies report large volume gains, ranging from 25-fold one year after planting to 80% after 10 years. Although the influence of weeds on tree growth declines with increasing age (Sands and Nambiar, 1984), there is some evidence to suggest that growth gains attained during the juvenile

phase are maintained throughout the length of the rotation (Snowdon and Khanna, 1989; Balneaves and McCord, 1990; Mason and Milne, 1999).

Construction of an accurate juvenile tree growth model sensitive to competition from weed species would enable managers to make informed decisions regarding vegetation management. Given the climatic and edaphic diversity of plantation sites within New Zealand, it would be advantageous if the model was widely applicable, yet not so complex that it is unsuitable for management applications.

Development of biologically realistic growth models requires specific knowledge of the mechanisms of interaction between trees and competitors, which will vary by site and weed species. One approach to understanding these interactions is to use a two stage process which involves investigation into how weeds alter resource availability, and how the trees respond to this change in resource availability (Goldberg, 1996).

Using this approach, mechanisms of juvenile tree suppression by a range of common weed species were investigated on a wet fertile site in the Central North Island, New Zealand. It was found that tall fast growing weed species on this site reduced *Pinus radiata* growth through restriction of solar radiation reaching the tree crowns. No convincing evidence was found to link the observed growth losses with competition by weeds for water or nutrients (Richardson *et al.*, 1996).

Data from this trial were used to develop a juvenile growth model sensitive to weed competition. A competition index, closely correlated to radiation availability, was derived from measurements of weed height relative to that of the trees, and weed abundance. This simple shade index was used to accurately predict tree growth in plots with and without weeds from the time of planting to age three (Kimberley and Richardson, 2001). In a further refinement, seasonal interactions between weed species and trees were incorporated into the model by Fourier series transformations (Kimberley and Richardson, 2003).

Although this model is suitable for wet sites, where weeds restrict growth primarily through light attenuation, it is not applicable to areas which experience seasonal water deficit. In dryland areas, weeds have been found to retard tree growth primarily through inducing water stress, and to a lesser extent through restriction of solar radiation reaching the tree crowns (see Chapter 2). The Central North Island model could be

modified for use on dryland sites through incorporation of an additional competition index, which accounts for weed competition for water.

Estimates of root-zone water storage, obtained from a water balance model may provide a useful process-based competition index for water. Water balance models have been included as components of highly parameterised process-based models to predict growth of mature *Pinus radiata* on dryland sites (Walcroft *et al.*, 1997; Arneth *et al.*, 1999). More recently these models have also been successfully used to account for growth loss in both juvenile (Watt *et al.*, 2003; Chapter 4) and mature stands of *Pinus radiata* (Richardson, *et al.*, 2003), subject to competition from the woody weed, broom (*Cytisus scoparius* L.).

The objective of this study was to develop a generally applicable juvenile tree growth model, sensitive to competition from weeds. Using data collected from a dryland site, this objective was achieved by (i) developing a competition modifier for water, based on root-zone water storage, estimated by a water balance model (ii) including this competition modifier in the existing Central North Island model developed for wet sites and (iii) testing the ability of this generalised model to accurately predict growth of *Pinus radiata* trees in plots with and without broom, on the dryland site.

METHODS

Site description

Measurements were taken over a two year period beginning June 2000, at an experimental site located near Hororata, 60 km west of Christchurch, New Zealand (latitude 43° 34' S, longitude 171° 55' E, 210 m asl). The soil on the site, which is classified as a stony Lismore silt loam, is shallow, free draining and of low fertility (Kear *et al.*, 1967). Water storage capacity within the very stony soil (21% by volume) is limited to approximately 70 mm in the main rooting zone (0.3 m soil depth). At depths lower than 0.3 m, volumetric stone content increases to over 50%, and root density is very low. Seasonal water deficits are characteristic of this soil and very common near Hororata as long term average rainfall is relatively low (797 mm yr⁻¹) and evaporative demand over spring and summer is high.

Experimental design and measurements

Experimental plots were located within a 20 ha *Pinus radiata* plantation established during winter 1999, at a spacing of 4 x 2 m (1 250 stems ha⁻¹). During the summer of 1999 twelve plots were established in areas where natural broom regeneration was high. The twelve plots were divided into six blocks. Plots within each block were randomly assigned to two treatments, which included no control of broom and complete removal of all broom. Each plot was approximately 12 x 24 m and included an interior 24 measurement trees, completely surrounded by buffer rows of seedlings.

Weed control was achieved by applying 6.25 kg of terbuthylazine mixed with 900 g of clopyralid and 300 g of haloxyfop in 250 l ha⁻¹ of water. This herbicide was applied to designated plots to eliminate existing vegetation, which consisted almost entirely of broom. After spraying, any weed regrowth was removed by a combination of hand weeding and spot herbicide application.

Meteorological sensors were installed on a 3 m tower, located in a small clearing adjacent to the experimental plots. Hourly measurements of incident irradiance, air temperature and relative humidity were made above the canopy. In treatment plots adjacent to the tower a tipping bucket raingauge on a 1.5 m stand measured above-canopy rainfall. Root-zone water storage in both treatments was recorded by two (one per treatment) time domain reflectometry sensors (Aquaflex, model SI. 60, Streat Instruments, Lincoln, New Zealand) installed within the tree rows, at a depth of 0.2 m.

Tree groundline diameter and height were measured at monthly intervals. At the same time height of the tallest eight broom plants within a one metre radius of the tree was measured, and averaged to determine the mean height, h_b . The proportion of ground covered by non-crop species, c_w , within a one metre radius of the tree was visually estimated every month.

Description of overall modelling approach

The modelling approach in this chapter extends that developed and described in detail by Kimberley and Richardson (2003). For trees in plots without broom the underlying trend in diameter growth was modelled using the simple power equation as,

$$A_d = r_1 t^{r_2} \quad (5.1)$$

where A_d is groundline tree diameter at time t and r_1 and r_2 are coefficients determined using a non-linear least squares regression procedure.

The seasonal influence on growth was modelled by superimposing the following single term Fourier series into Equation 5.1,

$$s(t) = \omega(\sin(2\pi(t + t_0 - t_m)) - \sin(2\pi(t_0 - t_m))) \quad (5.2)$$

where $s(t)$ is seasonally adjusted time, t_m is the time when growth reaches a maximum, ω is the amplitude of the seasonal effect, and t_0 is a reference starting point, when the series is constrained to equal 0 ($t_0 = 1 \text{ Jan } 2000$).

Equation 5.2 was incorporated into the growth function (Eq. 5.1) by using seasonally adjusted time, $t + s(t)$, in place of actual time, t , as,

$$A_d = r_1(t + s(t))^{r_2} \quad (5.3)$$

The influence of competition on tree growth can be incorporated into this model by,

$$A_d = m r_1(t + s(t))^{r_2} \quad (5.4)$$

where the term m is in effect a competition modifier that is equal to 1 when there is no competition (weed-free plots) and is reduced from 1 to 0, in the presence of competition (plots with weeds).

Kimberley and Richardson (2003) found that the most appropriate form of the modifier for light, m_l , was

$$m_l = 1 - (1 - e^{(z_1 c_1)})^{z_2} \quad (5.5)$$

where z_1 and z_2 were found to have respective values of -0.76 and 1.289. The competition index, c_1 , used in Equation 5.5 was calculated as,

$$c_l = \frac{h_b^2}{h_t^2} c_w \quad (5.6)$$

where h_b is mean broom height, h_t is height of the tree and c_w is the proportion of non-crop cover within a 1 m radius of the tree (Richardson *et al.*, 1999).

The modifier for water, m_w , was described by the following non-linear equation developed by Euan Mason (pers. comm.),

$$m_w = (1 - e^{(-q \theta_a)} + (\theta_a (e^{-q}))) \quad (5.7)$$

where θ_a is the fractional available root-zone volumetric water content, and q is an empirically determined parameter. Fractional available volumetric water content on day i ($= [(W_i - W_{\min}) / (W_{\max} - W_{\min})]$) was calculated from estimates of daily, maximum, and minimum root-zone water storage, in the treatment with broom. Measurements taken from a water sensor were used to define maximum, W_{\max} , and minimum, W_{\min} , values of root-zone water storage.

Daily root zone water storage, W_i , was calculated from Equations 4.1 to 4.5 using the water balance model described in detail in Chapter Four. Daily weather data required for the water balance model includes total rainfall, solar radiation, minimum and mean air temperature and average air saturation deficit. The model requires seasonal measurements of leaf area index for the trees, L_t , and broom, L_b . Values for the twelve parameters g_{stmax} , D_{0t} , g_{sbmax} , D_{0b} , θ_t , r , c , θ_{max} , θ_{min} , p_1 , p_2 , and p_3 , are given in Table 4.1, and based on measurements described in Chapter Four.

The combined competition modifier, m_c , was calculated as the product of m_l and m_w , and included in the following equation, which is the derivative of Eq. 5.4,

$$\frac{dA_d}{dt} = m_c (1 + 2\pi\omega \cos(2\pi(t + t_0 - t_m))) r_1^{(1/r_2)} r_2 A_d^{(1-1/r_2)} \quad (5.8)$$

Growth rate of trees in both treatments was modelled by Equation 5.8 using a monthly timestep. The competition modifier, m_c , was set to 1 for trees in plots without broom.

RESULTS

Parameterisation and validation of the water balance model

The total amount and distribution of rainfall varied considerably between the two years of the study (Fig. 5.1). The annual precipitation of 648 mm over the first year was well below average, while the 910 mm which occurred during the second year was considerably above average for this study area. During the first year only 28% of the annual total fell during summer and autumn and rainfall over the three month period from February to May was the lowest since records began in 1890 (Met Service database). In the second year 40% of the rainfall occurred (375 mm) during the very wet summer, and the remainder was evenly distributed throughout spring, autumn and winter (Fig. 5.1).

The average annual temperature during the first year (13.9°C) was slightly higher than that of the second year (13.5°C). Mean annual vapour pressure deficit varied 24% between the dry first year (0.62 kPa) and the relatively wet second year (0.47 kPa), with the most marked differences occurring over the summer months (Fig. 5.1). Incident irradiance totalled 2.4 GJ m⁻² during the first year, reaching maximum daily values in mid-summer. Although irradiance followed a similar seasonal pattern over the second year, the annual total was 15% lower (2.0 GJ m⁻²).

Broom leaf area index increased exponentially over time, from average values of 0.76 m² m⁻² in year 1 to 2.26 m² m⁻² during year 2 (Fig. 5.2). During both years L_b followed a regular seasonal pattern, reaching annual maxima during late summer, before steadily declining over autumn as a result of leaf loss (Fig. 5.2). Leaf area index of trees increased at a significantly lower rate. From starting values of 0.04 m² m⁻², L_t increased to respective values of 0.09 m² m⁻² and 0.18 m² m⁻² at the end of the first and second years (Fig. 5.2).

Modelled root-zone water storage corresponded closely to measured values over the two year period (Fig. 5.3). During the first year W declined rapidly from mid-spring onwards, nearly reaching minimum values (W_{\min} = 19.2 mm) by early-summer (Fig. 5.3). As rainfall was very sparse after this time W did not significantly increase from these minimum values until late autumn (Fig. 5.3). The above average rainfall during the second year caused considerable fluctuation in W , and average values during summer and autumn significantly exceeded those of the first year (41 vs 29 mm).

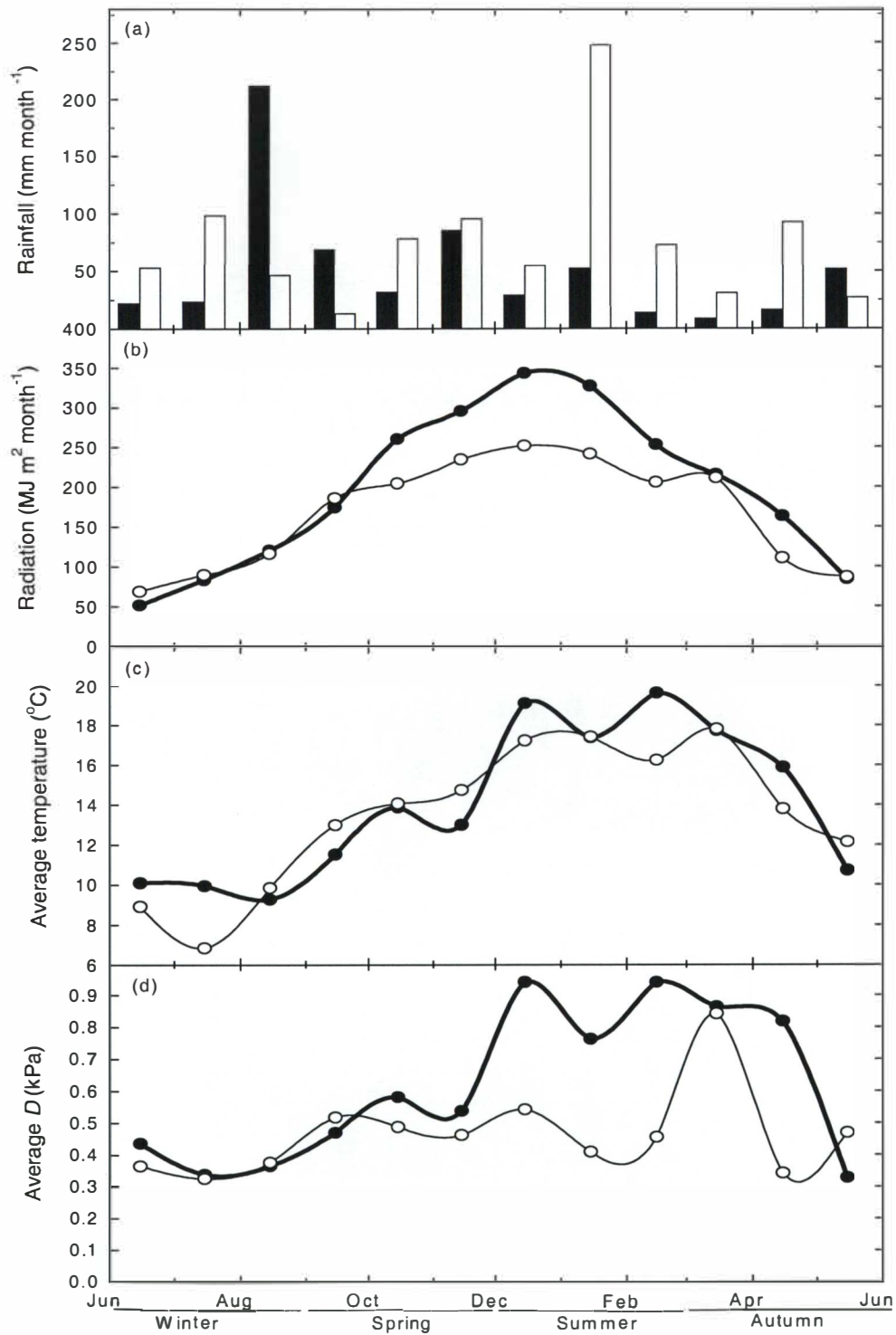


Figure 5.1. Seasonal changes in total monthly (a) rainfall and (b) radiation, and average monthly (c) temperature and (d) vapour pressure deficit during the first (filled symbols and bars) and second (open symbols and bars) years of the experiment.

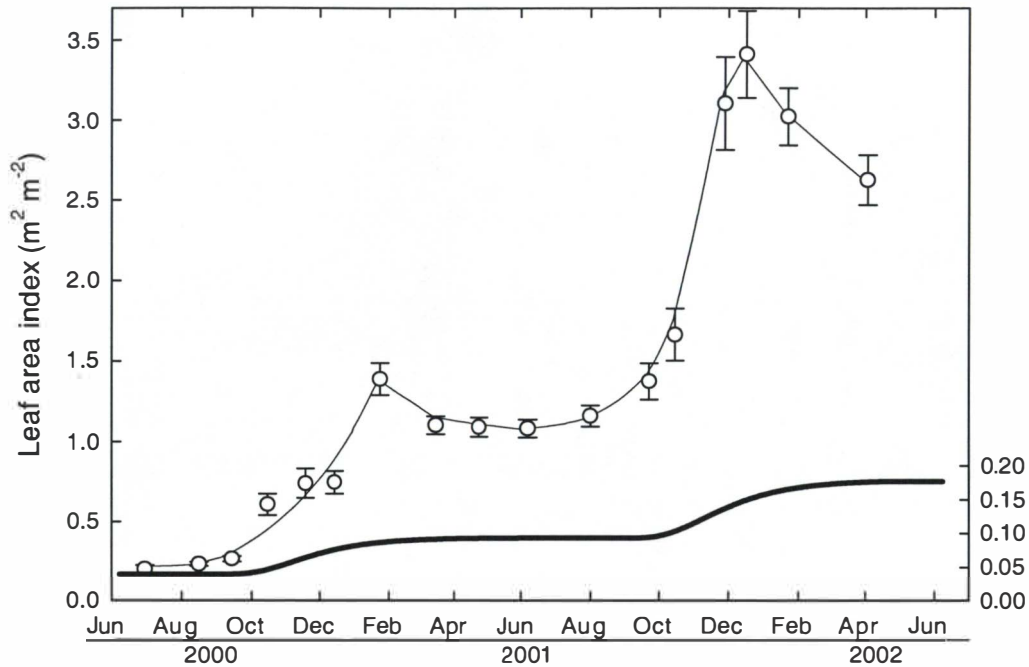


Figure 5.2. Seasonal changes in measured broom leaf area index (open circles). Also shown is modelled leaf area index for broom (thin line) and *Pinus radiata* growing in plots with broom (bold line). All leaf area indices are expressed on a half total surface area basis. Each measured point shown is the mean \pm standard error of six sample plots.

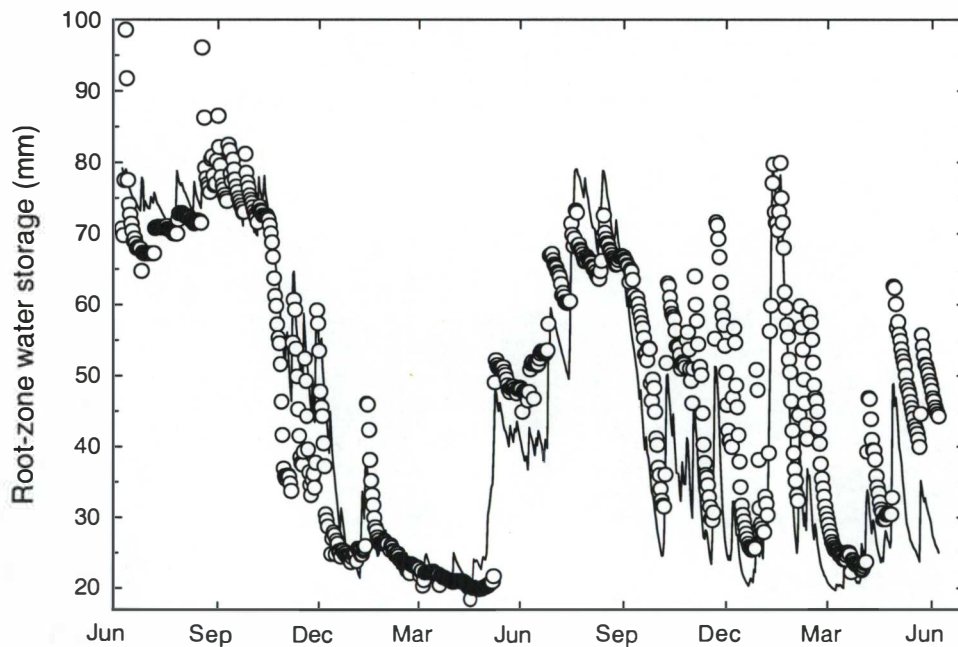


Figure 5.3. Comparison of modelled (continuous line) with measured (open symbols) root-zone water storage for a plot with broom, over the course of two years.

Modelling tree growth

The equation (Eq. 5.3) used to model diameter growth of *Pinus radiata* growing without broom fitted the data very well (Fig. 5.4). Total biomass increased exponentially over time and seasonal fluctuations in biomass growth exhibited a regular pattern during both years, with maxima occurring in early summer (t_m = December 25) and minima during winter (Fig. 5.4).

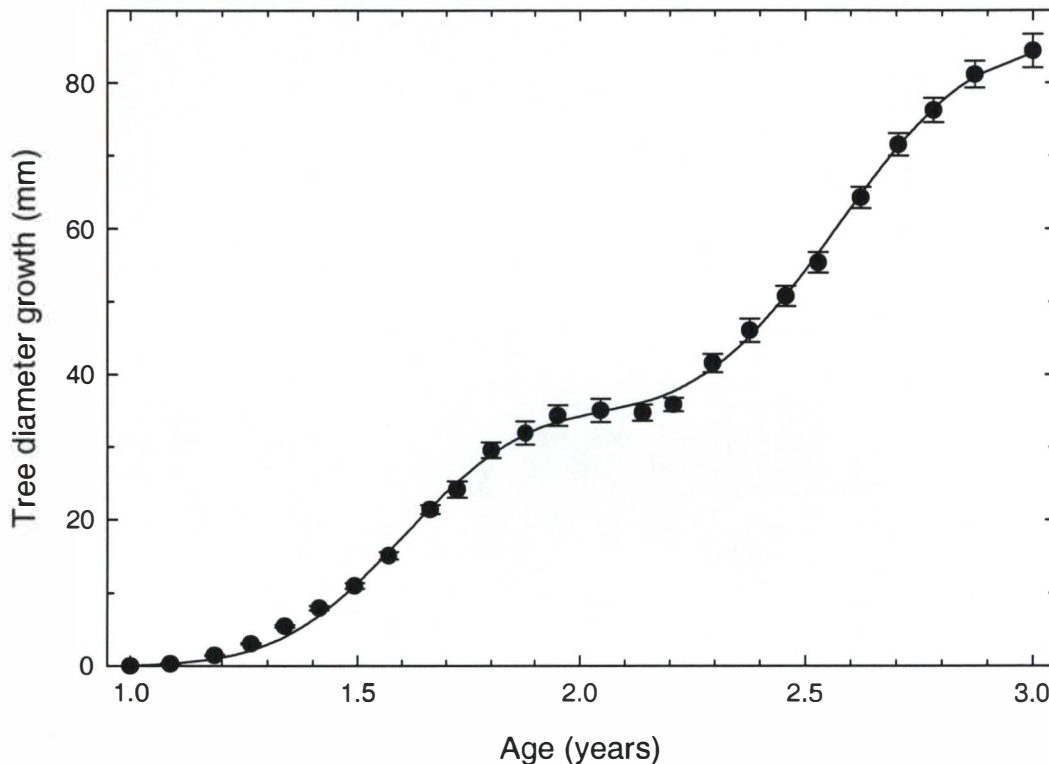


Figure 5.4. Seasonal changes in diameter growth for trees growing without broom (filled symbols) from age one to three. The line shows modelled diameter growth over the corresponding period. Each measured point shown is the mean \pm standard error of six sample plots.

The competition modifier for light (Eq. 5.5) developed in the Central North Island was incorporated into the weed-free growth function, and used to predict growth of trees in plots with broom. This modifier is based on the competition index (Eq. 5.6), c_1 , which increased significantly over the duration of the study, principally in response to changes in the proportion of ground covered by broom (Fig. 5.5).

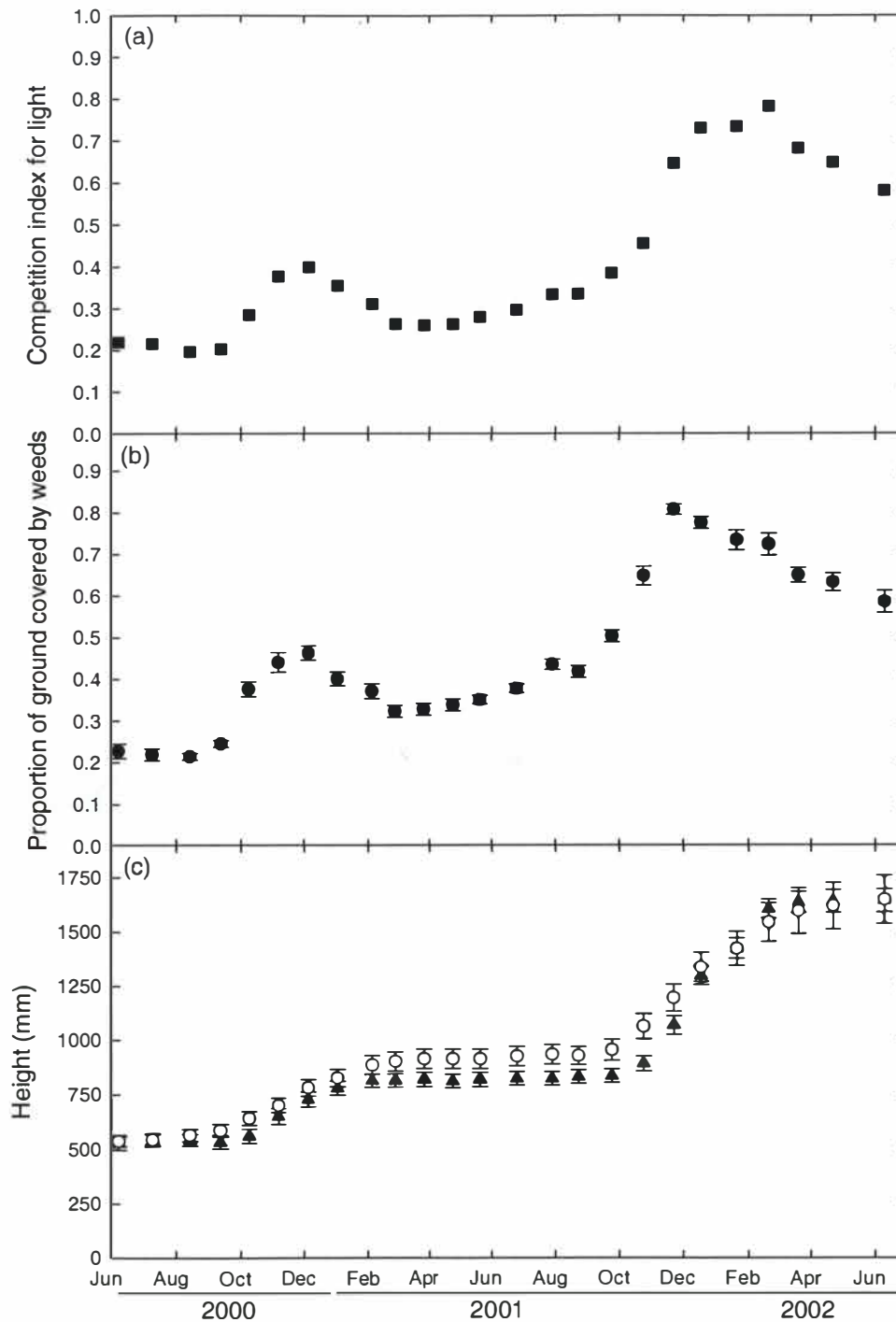


Figure 5.5. Seasonal changes in (a) competition index for light (b) proportion of ground covered by weeds and (c) height of broom (filled triangles) and *Pinus radiata* growing with broom (open circles). Each value shown is the mean \pm standard error of six sample plots.

Inclusion of the modifier for light reduced growth from that predicted for no competition (bold line, Fig 5.6) by 12% over the first year and 25% during the second year. However apart from the first few months this model significantly overpredicted measured diameter growth of trees in plots with broom (Fig. 5.6).

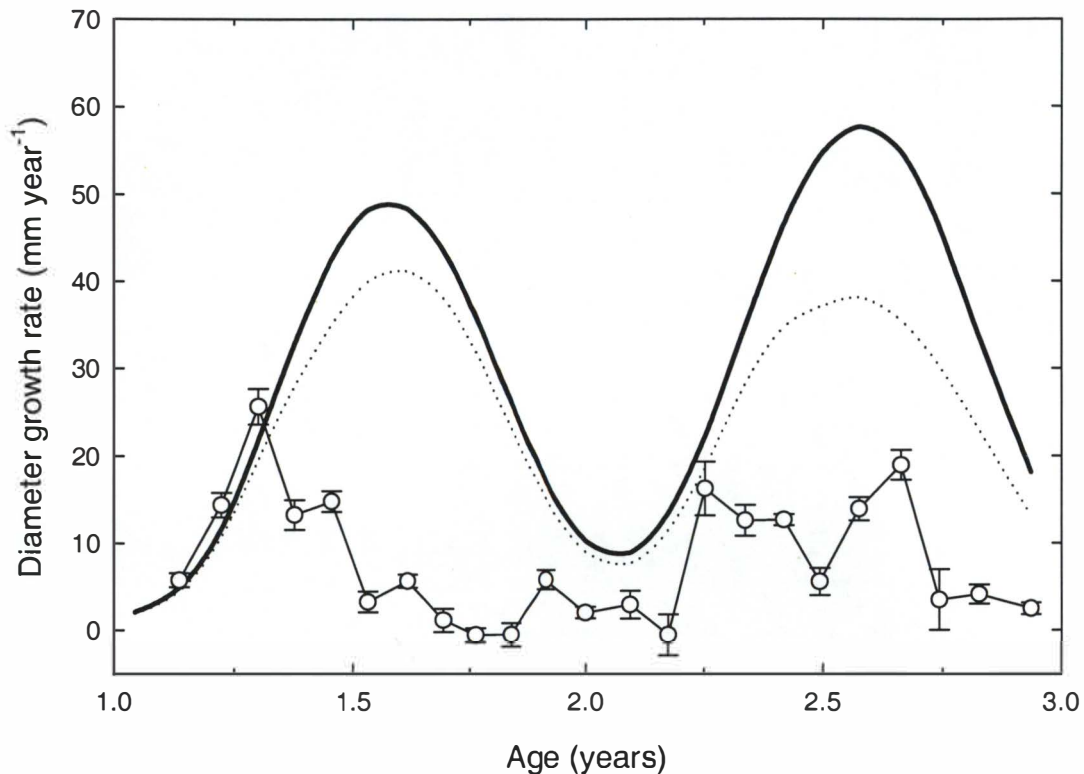


Figure. 5.6. Measured diameter growth rate of trees in the plots with broom (open symbols, thin line). Also shown is predicted growth for these trees assuming no competition for water or light (bold line) and competition for light (dotted line). Each measured point shown is the mean \pm standard error of six sample plots.

To account for the influence of water stress on growth a competition modifier based on modelled root-zone water storage was introduced into the model formulation. This model, described in Equation 5.8, consisted of the underlying power growth model, the seasonal model, and a combined modifier, calculated as the product of the light and water modifiers. Predictions of diameter growth using this model closely corresponded to measured diameter growth in both treatments (Fig. 5.7).

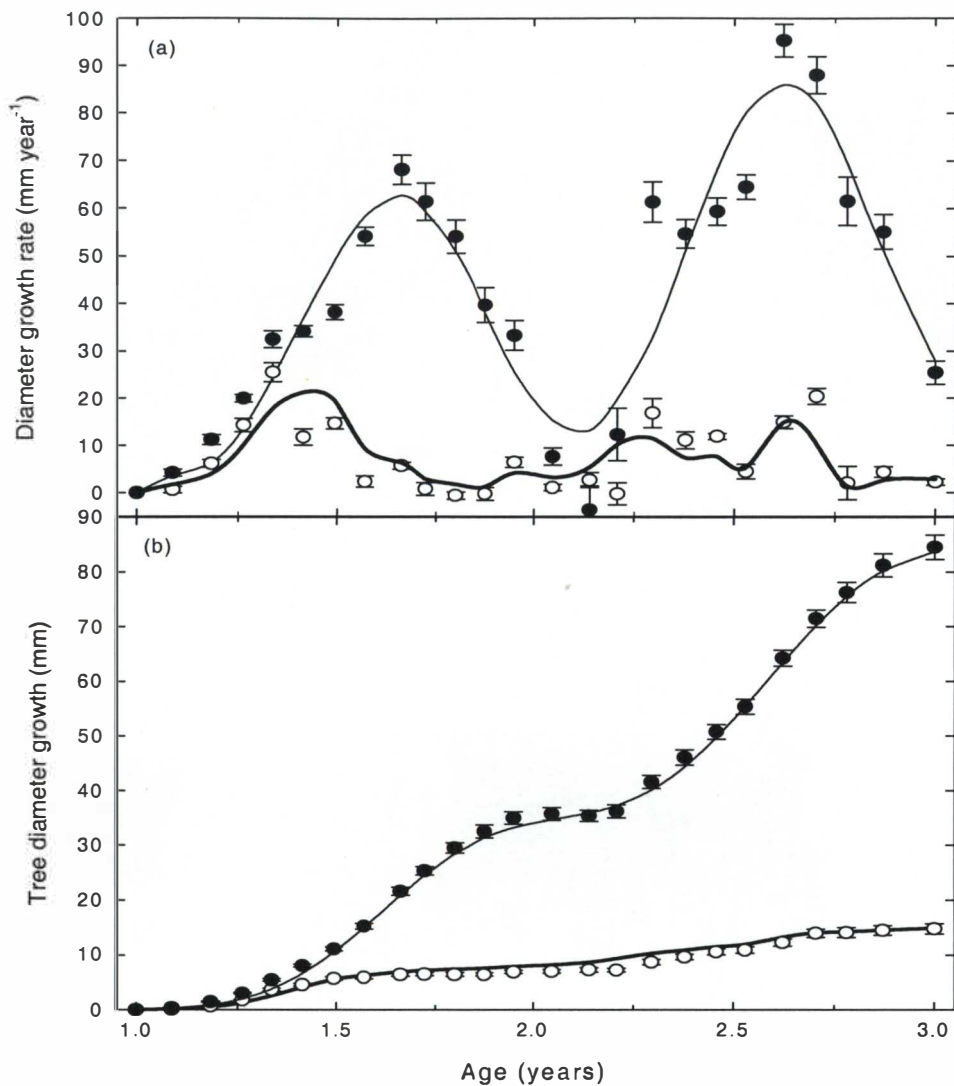


Figure. 5.7. Measured diameter growth and growth rate of trees from age one to three, in plots with (open symbols) and without (filled symbols) broom. Also shown are modelled predictions of diameter growth and growth rate for trees growing with (bold line) and without (thin line) broom over the corresponding period. Each measured point shown is the mean \pm standard error of six sample plots.

DISCUSSION

The model described in this paper, which was initially developed for wet sites, also successfully predicted tree growth at this dryland site when a competition modifier for water was included in the formulation. The ability of this modifier to successfully account for growth losses attributable to weed competition for water highlights the utility

of the water balance approach. As this model was developed at sites with contrasting conditions, using process-based modifiers for water and light, it should be applicable to sites covering a wide range of climatic and edaphic conditions.

Although this study indicates that the water competition modifier, m_w , is almost linear (Fig. 5.8), this form may to some extent depend on soil type. As soil hydraulic characteristics largely depend on particle size, it has been suggested (Landsberg and Waring, 1997) that at high values of θ_a the slope of m_w will progressively decrease as the ratio of clay to sand in the soil increases. Determination of the form of m_w over a broad range of soil types, with contrasting ratios of sand to clay would be useful.

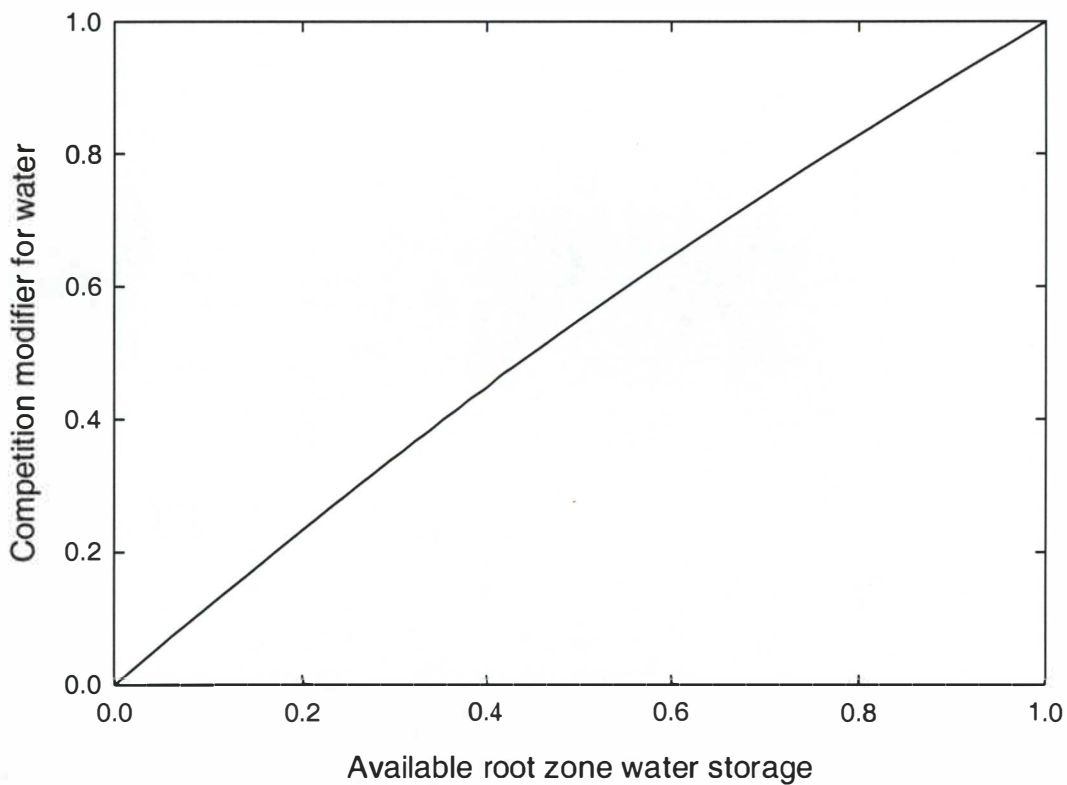


Figure 5.8. Competition modifier for water. The line shown was incorporated into the model (Eq. 5.8) by Equation 5.7, using a value for q of 0.7478.

Application of this modified model to the data enables the relative importance of broom competition for water and light to be quantified at this dryland site. Competition

for water had the dominant influence on tree growth, surpassing competition for light by seven-fold during the first year and two-fold over the second year.

The relative importance of weed competition for light and water will depend on both rainfall and root-zone water storage. On this particular site competition for water will always be the dominant mechanism as the shallow soil (0.3 m) has a low water storage, which is frequently exceeded by transpiration demand, even over wet years (e.g. year 2 in Fig. 5.3). In contrast, on wet sites in the Central North Island transpiration from broom is less likely to induce growth limiting seasonal water deficits as the soil has a high water storage. As a result tree growth in this region is restricted by weeds primarily through competition for light.

The model outlined in this paper is able to account for the seasonal interactions between tree and weed species. This approach is particularly advantageous when weeds and trees have different seasonal growth patterns, as even slight variations in growth between species may result in substantial changes in competition for light. This has been demonstrated on wet sites in the Central North Island where inclusion of seasonal interactions in the model was found to improve estimates of diameter growth loss for trees growing with a range of weed species (Kimberley and Richardson, 2003).

Use of short timesteps is likely to be even more critical for accurate estimation of m_w from the water balance model. As rainfall is unevenly distributed use of timesteps greater than one week may result in distorted estimates of evaporation, transpiration and drainage, which could seriously bias estimates of root-zone water storage. In contrast the model is likely to be less sensitive to the frequency of leaf area measurement. Although the model was parameterised from leaf area measurements taken at monthly intervals, there is likely to be little loss of accuracy if weed and tree leaf area is interpolated between seasonal measurements.

Use of this modelling technique assumes tree growth in weed-free plots was not constrained by water availability. This assumption is supported by the very regular seasonal pattern of biomass growth exhibited by trees in this treatment which closely approximated that of trees growing in irrigated weed-free plots in the Central North Island. This lack of a significant water limitation is further demonstrated by measurements of predawn needle water potential (ψ_e) which were relatively high (< -1 MPa), even during periods of severe drought (Chapter Two). Other studies on

dryland sites have also reported that water stress does not seriously limit growth of *Pinus radiata* in weed-free plots over the first three years following establishment (Sands and Nambiar, 1984; Richardson *et al.*, 1997).

Seasonal fluctuations in growth at this site were very similar to those recorded in the Central North Island. Maximum growth occurred within one week of the longest day (Dec. 21) in both regions. Although the amplitude parameter was found to be slightly larger on the dry Canterbury site (0.114 vs 0.083), the model was relatively insensitive to this difference. This similarity in seasonal growth between these two quite climatically different sites indicates that the model fitted in this study may adequately reflect seasonal growth patterns up to age three for most low altitude sites within New Zealand.

To conclude, this chapter presents a generally applicable juvenile tree growth model, which is sensitive to competition from weeds. This model predicts tree growth by reducing growth from an empirically determined optimum rate (weed-free) using a seasonally estimated competition modifier, which accounts for the degree of weed competition for both water and light. This model has considerable potential as a tool for managers to evaluate the cost effectiveness of alternative vegetation management regimes.

CHAPTER SIX

CONCLUDING REMARKS

This study highlights the importance of water in regulating productivity on dryland sites. The water balance approach was successfully used to simulate the influence of weeds on soil water storage, and these results were then used to construct a generally applicable model of tree growth, sensitive to weed competition. In the following discussion key findings are highlighted, and future directions and management implications of the modelling work are further outlined.

A principal result in Chapter Two was that almost all losses in tree growth at the experimental site were attributable to broom competition for either water or light. Results in Chapter Five indicated that competition by broom for water had the dominant influence on tree growth over the two year period, surpassing competition for light by seven-fold over the first year and two-fold during the second year. No convincing evidence was found to link losses in tree growth with broom competition for nitrogen.

It is not surprising that interspecific competition for water limited growth so strongly on this site, as it is located in an area characterised by low rainfall, shallow soils and high evaporative demand. Although water limitations at this site are at the severe end of the scale, almost all of the New Zealand plantation estate is subject to some degree of annual water deficit (Fig. 6.1). The only exception are the plantations located on the West Coast of the South Island, which comprise less than 2% (33 932 ha) of the national forest estate (Fig. 6.1).

It is likely that seasonal water deficits will be exacerbated by competing vegetation, which can significantly contribute to evaporative losses. This was clearly shown in Chapter Five where intense weed competition over the wet second year resulted in very high evaporative losses of 230 mm month⁻¹ during summer. Losses of this magnitude exceed corresponding summer rainfall inputs for almost all regions within New Zealand.

As the degree of water limitation will be highest on sites with low to moderate levels of rainfall, weed infested juvenile plantations in Hawkes Bay, East Coast, Marlborough, Canterbury and Otago are most prone to growth limiting seasonal water deficits (Fig. 6.1). Although seasonal water deficits become less marked as rainfall increases, trees growing in moderate to high rainfall areas are still subject to some degree of water limitation, particularly if rainfall is irregular and soil water storage low.

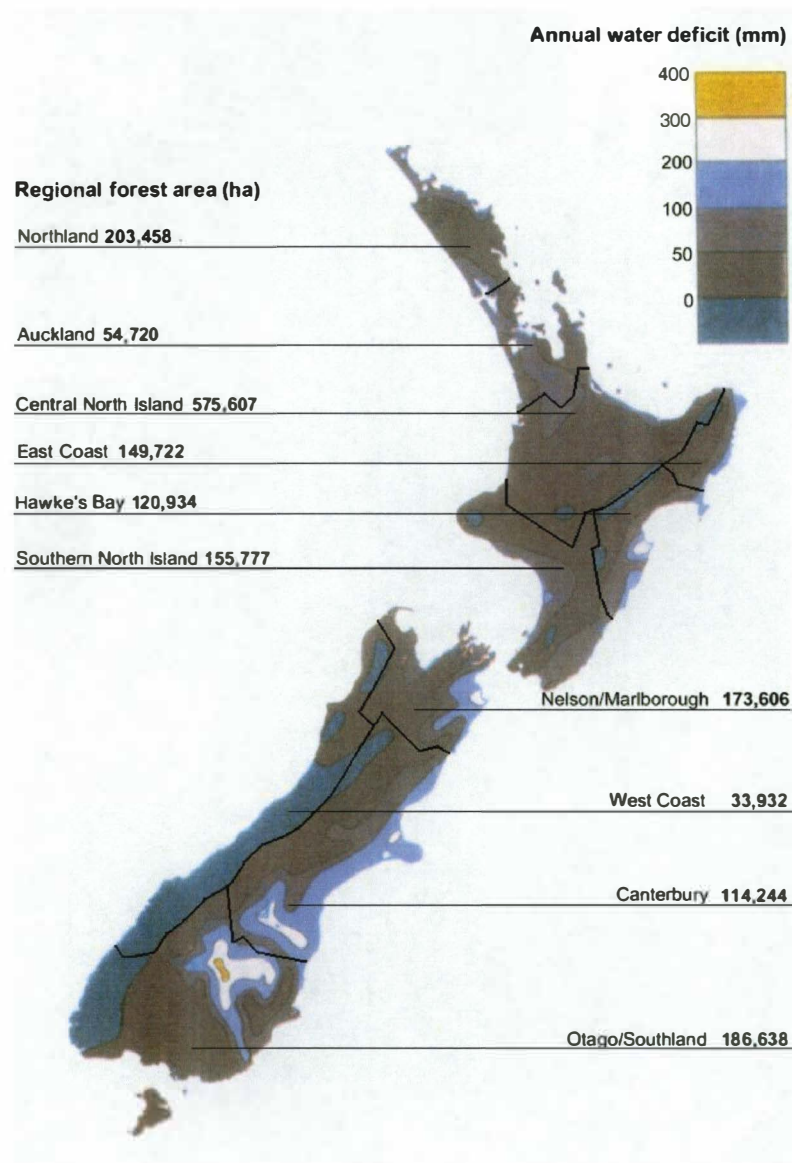


Figure 6.1. Map showing the annual water deficit in relation to the distribution of plantation forest, by region. For each region the area of plantation forest is shown. Adapted from New Zealand Atlas (1976), p. 89 and Forestry Facts and Figures 2002 p. 2.

The extensive plantations located in the Central North Island (Fig. 6.1) are least prone to growth-limiting water shortages, as rainfall in this region is high and evenly distributed and the deep pumice soil has a high soil water storage. However, even in this area, there are often dry periods over summer which can result in seasonal water deficits near the soil surface. These deficits are most likely to affect newly planted seedlings, where the root systems are often restricted to the upper soil layers.

In Chapter Four a water balance model was successfully used to model root-zone water storage, W , in both treatments during the first year. Application of this model to data from the second year, using parameter values determined in the first year, provided a successful validation of the water balance approach. As meteorological conditions varied considerably between the first and second year this validation also clearly demonstrated the responsiveness of this process-based approach to changes in environmental conditions.

Partitioning the components of water balance is useful as it enables the sensitivity of W to model parameters to be determined. In this study evaporative losses in plots with broom were mainly attributable to wet canopy evaporation, which accounted for 43% of total evaporative losses, over the two year period. As this is likely to be an important source of water loss for juvenile stands with tall, fast growing competitors, accurate estimation of W in these stands will require correct determination of this component. In contrast, transpiration from *Pinus radiata* in plots with broom was a very small component of water balance constituting only 1.5% of the total evaporative losses. As a result accurate determination of this component is not as critical for correct estimation of W .

Using insights gained from previous chapters a generally applicable model of juvenile tree growth, sensitive to competition from weeds, was successfully developed and tested in Chapter Five. This model which was based on the Central North Island hybrid model, included a competition modifier for water derived from the water balance model developed in Chapter Four. Inclusion of this modifier considerably improved the generality of the model as almost all plantation forest within New Zealand experiences seasonal water deficit to some extent (Fig. 6.1). Estimation of the modifier using a process-based approach highlights the extent of water limitation and explains differences

in tree growth over the range of weed species and site conditions found throughout New Zealand plantations. Further extension of the model presented in this thesis will provide a solid framework for predicting the influence of weed competition on juvenile tree growth.

In its current form the model is only suitable for trees growing with broom. Although broom is a very widespread weed species within New Zealand plantation forests, it would clearly be beneficial to extend the model to other common woody and herbaceous species. The type of weed species with which conifers compete can have an important influence on the level of water stress. Variation in water usage between weed species has been attributed to growth habit, physiological characteristics and depth of the root system (Sands and Nambiar, 1984; Richardson, 1993; Yusuna *et al.*, 1995). The water balance model developed in this study can be readily modified to accommodate alternative weed species, by obtaining species-specific parameter values for stomatal conductance characteristics, seasonal leaf area development, wet canopy evaporation and root depth.

The model described in this paper is only suitable for situations in which weeds are either completely removed or fully occupy the site. Given that aerial application of herbicide is the most extensively used method of weed control throughout Australia and New Zealand (Richardson, 1993), this is not seen as a major limitation. However the applicability of this model would be further improved if it were able to account for the influence of intermediate forms of weed control, such as strip or spot treatments, on tree growth. This could largely be achieved through development of a radiation transfer model which can partition light interception between trees and weeds with a complex spatial arrangement of foliage elements. Work on this model is already in progress.

Perhaps the most challenging modification would be development of a weed competition modifier for nutrient limitation. Accounting for this factor may be important in areas such as Northland where nutrient limitations of the infertile sandy soils are a major constraint to tree growth (South and Skinner, 1998). A large part of this growth restriction may be accounted for through accurate definition of tree growth in weed-free plots, using either empirical means or process-based models.

Competition by weeds for nitrogen on these sites may prove to be more difficult to define. The amount of nutrients accumulated and released by weeds varies considerably, depending on a range of factors including rates of biomass accumulation, and decomposition, species diversity, stand age, and site management practices (Nambiar and Sands, 1993). Predicting these nutrient fluxes is further complicated on drier sites as seasonal water deficits almost always impair nutrient uptake. The influence of nitrogen fixing weeds on tree growth is likely to depend on rates of fixation, availability of soil nitrogen and levels of soil water storage. In general it seems likely that benefits will accrue from nitrogen fixing species only when the site is deficient in nitrogen and not significantly limited by seasonal water deficit (Richardson, 1993).

Clearly, the establishment of well designed experiments in which tree growth is limited by nutrients but not water availability would provide a better understanding of these complex competitive processes. Application of the model developed in this study to these data would provide one means of quantifying nutrient constraints on tree growth. This would be a useful first step in development of an additional competition modifier.

The model presented in this paper could be readily applied to management situations as it has relatively low input requirements. Daily meteorological data are readily available for most locations. Geographical information systems (GIS) can be used to map the requisite information on soil characteristics, at a fine resolution. The other physiological parameters detailed in this paper would be supplied with the model. Although it is relatively easy to parameterise two adaptations have potential to further simplify this model.

It is recommended that the weed-free tree growth curve be calibrated for a specific site before the model is used for management applications. In the simplest case, site calibration would involve a single measurement of tree height and diameter, preferably taken near the end of the juvenile period. As this type of information may be difficult for forest managers to obtain, further research should aim to characterise weed-free tree growth over a range of site conditions. These data could then be used to either (1) empirically determine parameters for the current model over a range of regions or (2) develop a more process based weed-free tree growth model which is generally applicable.

One way of simplifying estimation of the water competition modifier, m_w , without unduly compromising accuracy would be to undertake a project where W is estimated by the water balance model throughout New Zealand forests, for the most commonly occurring weed species. From these runs a relationship between weed leaf area and soil water storage could be developed for each site, and linked into GIS. Through utilisation of this information, user inputs for m_w could potentially be reduced to site location, weed species and percentage cover at one point in time.

These modifications are likely to improve future models. However as it stands the model presented in this thesis provides a sound framework for modelling the influence of weeds on juvenile tree growth over sites covering a wide range of climatic and edaphic conditions.

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